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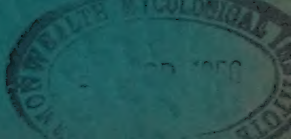
AUSTRALIAN JOURNAL OF AGRICULTURAL RESEARCH

VOLUME 7
NUMBER 2
MARCH 1956

REGISTERED IN AUSTRALIA FOR TRANSMISSION BY POST AS A PERIODICAL



AUSTRALIAN JOURNAL OF AGRICULTURAL RESEARCH

Published by the Commonwealth Scientific and Industrial Research Organization, in collaboration with the Australian Institute of Agricultural Science, and the Australian Veterinary Association, and under the general direction of the Editorial Board (Dr. N. S. Noble (Chairman), Professor J. S. Anderson, Professor Sir Macfarlane Burnet, Professor L. H. Martin, and Professor J. G. Wood). A medium for the publication of results of original investigations in the broad field of scientific research on plants, soils, and domestic animals, covering physical, chemical, and biological aspects of this field

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MELBOURNE

LEGUME "LITTLE LEAF", A VIRUS DISEASE OF SUBTROPICAL PASTURE SPECIES

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(*Manuscript received October* 21, 1955)

Summary

A virus of legumes causing a disease described as "little leaf" has infected with differing degrees of severity some 40 per cent. of pasture legumes in experimental plots in subtropical Queensland. The symptoms are similar to those caused by the "big bud–witches' broom" complex of viruses of which it is probably another strain. Transmission studies have shown that the vector is the leafhopper *Orosius argentatus* (Evans) which also transmits tomato "big bud", lucerne "witches' broom", potato "purple top wilt", and tobacco "yellow dwarf" diseases. The *O. argentatus* taken direct from the field in Queensland, and its progeny reared in the laboratory, were efficient vectors of "little leaf" whereas the Canberra strain bred in the laboratory would not transmit "little leaf" and was not an efficient vector of the other "yellows" viruses.

The majority of species and strains tested in the genera *Crotalaria, Desmodium, Indigofera,* and *Stylosanthes* are susceptible to "little leaf". Within such genera there are a few resistant species or strains with promising agronomic characters. Lucerne and white clover are relatively resistant to "little leaf". The genera *Arachis, Centrosema, Dolichos, Glycine, Lespedeza, Leucaena, Pueraria, Phaseolus, Vigna,* and *Zornia* contain species and strains with marked field resistance. Most of the species and strains considered to be promising pasture legumes possess field resistance to "little leaf".

I. INTRODUCTION

At Strathpine Experiment Station, C.S.I.R.O., near Brisbane, a comprehensive range of legumes from South and Central America, Africa, Hawaii, and India has been grown. The most destructive disease which has appeared in them has been called "little leaf" because of its symptoms. This disease has occurred in a number of other areas of coastal and subcoastal Queensland. In 1954, at Beerwah, 50 miles north of Brisbane, "little leaf" appeared within 4 months of seeding in a plot of the stoloniferous *Desmodium uncinatum* (C.P.I.‡ 8990) isolated in a forest reserve. The mode of occurrence of "little leaf" suggested its spread from indigenous and naturalized plants by an insect vector. All the general evidence indicated that "little leaf" has been widespread among legumes in the subtropical and tropical areas of Australia for a number of years.

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‡ Commonwealth Plant Introduction.

Field symptoms of the disease indicate that it is probably closely related to the lucerne "witches' broom" virus disease, of which the leafhopper *Orosius argentatus* (Evans) is the insect vector. Four other yellows viruses transmitted by leafhoppers have been recorded in Australia, but only three are important diseases of legumes. Hill (1943) recorded *O. argentatus* as the vector of tomato big bud and showed that the host range included many legumes. Hill and Helson (1949) reported *O. argentatus* as the common vector of three plant viruses, tomato "big bud", lucerne "witches' broom", and tobacco "yellow dwarf". Helson (1951), as the result of insect and graft transmission to a large number of plant hosts, concluded that the first two diseases were caused by the same, or strains of the same, virus. The other important virus affecting legumes, which appears to be quite distinct, is rugose leaf curl (Grylls 1954). This virus disease and the leafhopper vector *Austroagallia torrida* (Evans) are present in Queensland and have been recorded from areas where "little leaf" is also present (Grylls 1955). A "little leaf" disease of brinjal has been reported in southern India (Thomas and Krisnaswami 1939) as being transmitted by the leafhopper species *Eutettix phycitis* Distant. Oman (1949) states that this species does not belong to the genus *Eutettix*. However, other leafhoppers belonging to the same group as *phycitis* have been recorded in Queensland (Evans 1938).

The purpose of this paper is to describe the symptoms of "little leaf", to define its insect vector, and to record its occurrence on legumes during three seasons at the Strathpine Experiment Station. The problem of field resistance to the disease is also discussed. Work reported in this paper was done partly at Brisbane and partly at Canberra.

II. Symptoms of the "Little Leaf" Disease

(*a*) *In the Field*

The first recognizable symptoms in the field were a marginal and interveinal chlorosis and a puckering of the leaves which usually developed a few months after planting. If the plants were flowering, green distorted buds appeared on some branches while other branches flowered and seeded normally. Green flowers as may occur with "big bud" and "witches' broom" were not observed. It was of some significance that tomatoes grown adjacent to "little leaf"-infected legumes at Strathpine Experiment Station did not develop "big bud" symptoms.

The terminal buds of infected shoots produced small rounded leaves which were lighter green in colour than those of healthy plants. This phase was often followed by the production of relatively large numbers of small spindly shoots with leaves markedly reduced in size. Proliferation of shoots from the leaf axils could occur anywhere on the plant. Infected plants of the more upright species, such as the glossy-leaved strains of

Desmodium uncinatum, sometimes had a lopsided appearance due to proliferation at the base on one side.

Plate 1, Figures 1 and 2, compare healthy and diseased plants of *Crotalaria intermedia* (C.P.I. 1254) and *D. uncinatum* (C.P.I. 11740).

Most infected plants of *D. canum* and the upright strains of *D. uncinatum* died in two seasons. In the other perennial species infected plants gradually died, but not as rapidly, so that 5 to 80 per cent. of the diseased plants were still persisting after two seasons. In two strains of *Stylosanthes gracilis* (C.P.I. 11490 and C.P.I. 11491), 80 per cent. of the diseased plants persisted in an appressed condition for three seasons, the growth being yellow and proliferated and the leaves markedly dwarfed. Diseased plants of the annual species, confined mainly to the genus *Crotalaria*, often died prematurely.

(*b*) *In Glass-house Transmission Experiments*

The proven vector *O. argentatus* (see later) was used for the glass-house transmission experiments of "little leaf". Primary symptoms in seedling legumes occurred 8-10 days after the infection feed and consisted of marginal chlorosis, leaf puckering, and the production of smallish rounded leaves. However, in the majority of plants the primary symptoms disappeared after a few days and the severe and more typical field symptoms appeared. These varied slightly with plant species and age at which they were infected. In older plants symptoms consisted of distinct proliferation from the growing tips or leaf axils. Small leaves were produced with thin petioles. Clover plants infected at the "four leaf" stage became extremely stunted and proliferation took place at the crown of the plants. The red clover and lucerne plants referred to in Table 2 were well grown when infected and severe symptoms took a long time to develop. The transition from primary to severe symptom expression was gradual, particularly in lucerne, hence the periods quoted are only approximate. Early primary symptoms were not noted on plants other than legumes, and other symptoms took longer to appear. The apparent temporary recovery of legume species was not observed in tomato or *Datura* nor in carrot. It is possible that primary symptoms did develop at an earlier stage on these plants but were not recognized as such.

When the disease was transmitted from *Datura* to tomato and *Datura*, and from tomato to tomato by graft, symptoms developed in approximately the same period of time as on other plants grafted with scions from "big bud-witches' broom"- and potato "purple top"-infected plants. Symptoms of "little leaf" on the above hosts differed slightly from those of the other two viruses in the early stages of development but the plants later developed green flowers characteristic of the "big bud-witches' broom" complex.

III. Insect Vector

(a) *Field Survey*

A field survey of the leafhopper fauna was commenced in June 1954. Plots of *Arachis prostrata, D. uncinatum,* and *Lotononis bainesii* were selected and each of these was swept 50 times at fortnightly intervals with a 14-in. organdie net. Although *O. argentatus* and *A. torrida* appeared to show a preference for *L. bainesii* and *D. uncinatum* in that order, the trend over the season was not significant. Table 1 records the total number of each of the leafhopper species found on the three legume species at each fortnightly sweeping.

Table 1

TOTAL NUMBERS AND SPECIES OF LEAFHOPPERS TAKEN IN 50 HAND SWEEPS OVER THREE SPECIES OF LEGUMES AT STRATHPINE AT FORTNIGHTLY INTERVALS

Leafhopper Species*	Number of Leafhoppers Taken†											
	June 1954	July 1954	Aug. 1954	Sept. 1954	Oct. 1954	Nov. 1954	Dec. 1954	Jan. 1955	Feb. 1955	Mar. 1955	Apr. 1955	May 1955
O. argentatus	0	0	0	0	0	7	1	5	2	1	0	0
	1	1	0	0	23	4	4	1	1	0	0	0
A. torrida	0	8	2	5	8	5	5	15	2	0	4	0
	5	5	1	7	0	3	10	0	3	1	0	2
C. bimaculata	0	1	1	0	0	1	1	0	0	0	2	1
	1	1	0	0	0	0	0	0	1	2	0	0
Balclutha spp.	0	21	40	51	0	6	4	130	33	24	91	694
	9	10	1	0	1	13	23	0	82	64	284	29
Other spp.	0	6	3	3	0	5	4	16	0	5	6	1
	7	3	4	0	8	1	8	0	10	7	0	1

* Other species taken include: *Eurinoscopus punctatus* (Evans); *Austroasca* spp.; *Exitianus norrisi* (Evans); *Cicadella albidula* Walk.; *Euscelis* sp.

† For each species, upper and lower values for each month refer to numbers taken in first and second sweeps of the month respectively.

Of the species listed in Table 1, *O. argentatus* and *A. torrida* have already been referred to as vectors, and *Cicadulina* (= *Cicadula*) *bimaculata* (Evans) has been recorded by Schindler (1942) as a vector of wallaby ear of maize in Queensland. Of these three species *A. torrida* occurred in the greatest numbers and was distributed most evenly through the year, although the increase in numbers of *O. argentatus* in the spring and early summer coincided with the appearance of "little leaf" in the field. The most numerous leafhoppers in the collections were *Balclutha* spp., including *B. sanguinescens* Kirk., and these are considered to be mainly grass feeders.

(*b*) *Identification*

Attempts were made in Canberra to transmit the virus by means of laboratory-reared leafhoppers derived from Canberra stock. Several tests were made using *O. argentatus* with acquisition feeds of 24 hr to 6 days, and infective feeding periods of 2-7 days. These tests covered possible incubation periods of the virus in the insect of up to 4 weeks. No transmission resulted from these tests although this culture had previously transmitted the other viruses of the "big bud–witches' broom" complex. Less extensive tests were done with *A. torrida* but again no transmission occurred.

TABLE 2

TRANSMISSION OF "LITTLE LEAF" VIRUS BY *O. ARGENTATUS* SHOWING INCUBATION PERIOD IN VARIOUS HOST PLANTS

Host Plants	No. of Plants Used	No. of Plants Infected	No. of Days for Development of	
			Primary Symptoms	Severe Symptoms
Desmodium uncinatum, C.P.I. 8990	9	8	7	45
D. uncinatum, C.P.I. 11740	6	4	9	63
Trifolium pratense var. New Zealand certified	2	1	14	103
T. subterraneum L. var. Mt. Barker and Wenigup	22	20	7-10	32
Medicago sativa var. Hunter River	8	5	10	150
Malva parviflora L.	4	2	7	28
Lotononis bainesii, C.P.I. 16833	2	2	17	45
Lycopersicon esculentum Mill. var. Rouge de Marmande	6	2	35	55
Datura stramonium L.	5	2	102	123
Daucus carota L. var. Chantenay	4	2	91	101

In October 1954, collections were made of leafhoppers from legume plots at Strathpine Experiment Station. *O. argentatus* and *A. torrida* species were isolated and caged separately for 7 days on healthy plants of the susceptible legumes, *D. uncinatum* and *C. intermedia*. Similarly a composite group of these two leafhoppers collected from C.S.I.R.O. plots at Beerwah were also caged on the two susceptible species, as were other leafhoppers including *Eurinoscopus punctatus* (Evans), *Exitianus norrisi* (Evans), *Cicadulina bimaculata*, and *Balclutha* spp. "Little leaf" symptoms appeared on all plants on which *O. argentatus* were caged, primary symptoms developing in 8-10 days, but no virus symptoms appeared in

plants fed on by other leafhopper species. When the *Orosius* and *Austroagallia* leafhoppers from the Strathpine Experiment Station and Beerwah collections were separated and the species caged separately, the former species transmitted the virus but the latter failed to do so.

In the insectary in Canberra the various leafhopper species were later tested on a number of plant species. No transmission was effected by any species other than *O. argentatus*. The virus was transmitted only by *O. argentatus* collected in Queensland, and by their reinfected progeny. The incubation periods of the virus in the various hosts are shown in Table 2.

IV. Field Susceptibility and Resistance of Species and Strains of Legumes

(*a*) *Susceptibility*

A preliminary survey of the incidence of "little leaf" among the legumes growing in the plant introduction plots at Strathpine Experiment Station was made during 1953. In most instances the plots had been established for at least a year so that sufficient time had elapsed for a natural infection of "little leaf" to have developed. The survey showed that there was a range in susceptibility of species and that a number of species and strains was resistant. During the 1954 and 1955 seasons infected plants were counted and rated for severity of the disease. Most of the species and strains were in cultivated rows 16 ft long and 4 ft apart; half were in triplicate, some in duplicate, and the least important in single rows. The 11 most important species were also grown in plots 1 sq. chain in area containing several thousand plants. Thus the number of plants available for observation varied considerably, the number in the smaller plots ranging from 10 to 171, with a mean of 70. Strains given a rating of 1 showed interveinal chlorosis of leaves, some reduction in leaf size, and some stem proliferation. At the other extreme, a rating of 5 was given to severely affected species or strains which were greatly reduced in growth and which possessed small chlorotic leaves and extensive proliferation of small spindly shoots. The observations are summarized in Table 3.

It is apparent from Table 3 that a comprehensive range of species became infected with "little leaf" and that in about 60 per cent. of them there was a high percentage of infection often coupled with severe symptoms. The rate of spread of the disease was slow within some species, particularly with lucerne (*Medicago sativa*) and red and white clovers (*Trifolium pratense* and *T. repens*). In one area of lucerne containing 1000 plants only 1 per cent. of the plants became mildly infected over a 12-month period in which other species became heavily infected. Pigeon pea (*Cajanus cajan*) is another species in which the disease spreads slowly; infected plants often appear normal, symptoms being confined to one or two side branches.

TABLE 3 (*Continued*)

OCCURRENCE OF "LITTLE LEAF" INFECTION IN LEGUMES AT STRATHPINE EXPERIMENT STATION DURING THE 1954 AND 1955 SEASONS

Species	C.P.I. Number*	No. of Plants Examined	% of Infected Plants in Plots		Severity Rating†
			1954	1955	
Aeschynomene falcata (Poir.) DC.	11500	58		1	2
Astragalus glycyphyllus L.	12494	28	40	50	3
Cajanus cajan (L.) Millsp.	15142	12	5	24	3
	17178	51	25		2
	17179	10	10		2
	17433	32	25	27	2
Crotalaria goreensis Guill. & Perrott	1251	60		60	2
Crotalaria grahamiana Wight & Arn.	13378	59	25		1
Crotalaria intermedia Kotschy	1254	55	100		4
Crotalaria juncea L.	15417	61		2	2
Crotalaria orixensis Willd.	13698	46	90		4
Crotalaria pumila Ortega	13699	58	80		4
Crotalaria retusa L.	1257	53	80		4
Crotalaria sericea Retz.	5775	32	100		5
Desmodium batocaulon A. Gray	12346	40	67	—‡	4
Desmodium canum (J. F. Gmel.) Schinz & Thell.	11739	56	50	—	5
	11792	59	100	—	5
	18006	50		75	4
Desmodium gangeticum (L.) DC.	13170	28	21	25	3
Desmodium uncinatum (Jacq.) DC.	8990	3100	72	—	4
	11740	322	100	100	2-5
	18011	52	4	100	2-5
Desmodium scorpiurus (Sw.) Desv.	15420	49	22	—	3
	17184	61	60	—	3
	15421	58	90	—	4
Dolichos striatus Steud.	17082	55	82	—	4
Indigofera endecaphylla Jacq.	15733	60	60	70	3
	16110	51	65	90	2
	16069	59	Nil	1	1
	16674	38	60	78	4

* Commonwealth Plant Introduction.

† 1, Mild. 5, Very severe.

‡ A dash in the results for the 1955 ratings indicates that the introduction had died out.

TABLE 3

Species	C.P.I. Number*	No. of Plants Examined	% of Infected Plants in Plots		Severity Rating†
			1954	1955	
Indigofera retroflexa Baill.	16678	24	30		1
Indigofera subulata Vahl	17810	28		3	1
Indigofera tettensis Klotzsch	16055	31	Nil	51	3
Indigofera species§	15734	29	Nil	90	1
	16174	34	22	100	2
	17261	52	80	—‡	4
Lathyrus sylvestris L.	13360	55	20	—	1
Lotononis bainesii R. T. Bak.	16833	138	65	75	3
	17085	164	51	72	3
Medicago sativa L.		74	13		1
		1000		1	1
Rhynchosia hagenbeckii Harms	11835	25	80	90	4
Rhynchosia minima (L.) DC.	12365	56	50	50	3
Stylosanthes bojeri Vog.	15097	54	48	—	2
Stylosanthes erecta Beauv.	16511	79	100	—	2
Stylosanthes gracilis H.B.K.	11490	143	55	60	2
	11491	138	75	84	3
	11493	2081	61	84	3
	11497	161	100	100	3
Stylosanthes guianensis Sw.	11846	133	Nil	51	2
Stylosanthes leiocarpa Vog.	11498	66	30	31	2
Stylosanthes montevidensis Vog.	11492	58	50	82	3
Stylosanthes sundaica Taub.		120	50	90	2
		107		29	2
Stylosanthes species§	11849	123	30	35	3
	15746	171	80	—	4
	17210	154	72	—	4
Tephrosia species§	16111	39	15		3
Trifolium pratense L.		1100		2	2
Trifolium repens L.		2700	5	5	2

* Commonwealth Plant Introduction.

† 1, Mild. 5, Very severe.

‡ A dash in the results for the 1955 ratings indicates that the introduction had died out.

§ Where the specific name is not given, identification of the species has not been completed.

Table 3 shows that a high proportion of the species and strains which have been tested in the genera *Crotalaria, Desmodium, Indigofera,* and *Stylosanthes* was susceptible. The genus *Crotalaria* does not contain any

impressive pasture species, but species and strains within the other three genera have shown distinct promise in preliminary trials. *D. canum*, which has done well in Hawaii (Hosaka 1945), was killed out in our plots within 3 years by "little leaf". The upright glossy-leaved type of *D. uncinatum* (e.g. C.P.I. 11740, 18011) also became infected and few plants remained after 2 years. Surviving plants of both *D. canum* and the glossy-leaved *D. uncinatum* were invariably infected and their seedling progeny showed no resistance to the disease when planted in the field.

D. uncinatum (C.P.I. 8990), a promising stoloniferous form, has the unusual ability of being able to grow away from "little leaf". When its rate of growth is slow, as in spring or late autumn, plots of this strain are often severely affected. In the same plots during midsummer the plants grow vigorously and form a large bulk of stems and leaves apparently free from infection. Examination of infected plants shows that stolons may develop from diseased crowns or shoots. These may root and a vigorous plant develop independently of the parent.

Most of the species and strains of *Indigofera* and *Stylosanthes* listed in Table 3 became relatively heavily infected. In the majority of the *Stylosanthes* introductions and in *Lotononis bainesii* affected plants showed a marked stunting and proliferation. *L. bainesii* is a promising legume which is quite susceptible to "little leaf", no resistant strains having been found as yet.

Fairly rapid death of plants following infection occurred in the field in glossy-leaved *D. uncinatum* and in *D. canum*. Infected plants in other species continued growth at a diminished rate and died more gradually, although in a number, as shown by the dashes in Table 3, the rows had died out by the 1955 rating.

(*b*) *Resistance*

In Table 4 species and strains of legumes which have remained free of "little leaf" or which have shown a high degree of field resistance to the disease are listed.

It is apparent when Tables 3 and 4 are compared that, with one exception, the species and strains under test in the important genera *Arachis, Centrosema, Dolichos, Glycine, Lespedeza, Leucaena, Pueraria, Phaseolus, Vigna*, and *Zornia* were field-resistant. In addition, the genera in which the majority of species tested were susceptible usually had one or two species or strains which were quite resistant. This is noticeable particularly in *Desmodium, Indigofera*, and *Stylosanthes*. *D. intortum*, a stoloniferous type, was highly resistant although an occasional mildly infected plant was observed. The naturalized *D. triflorum* DC. also appeared to be quite resistant, while in *I. endecaphylla* the most promising strains C.P.I. 11412, 12240, and 15362 were the most resistant. *Stylosanthes* species and strains which were resistant possess similar agronomic characteristics to those of the susceptible ones.

TABLE 4

SPECIES AND STRAINS OF LEGUMES WITH FIELD RESISTANCE TO "LITTLE LEAF" INFECTION

Species	C.P.I. Number*
Alysicarpus longifolius (Rottl.) Wight & Arn.	16671
Arachis diogoi Hoehne	8987
	8988
Arachis prostrata Benth.	12121
Cajanus cajan (L.) Millsp.	13128
	14580
	14583
	16107
Calopogonium mucunoides Desv.	16858
Centrosema pubescens Benth.	16416
	16862
	16863
Cassia rotundifolia Pers.	16358
Crotalaria species†	17182
Desmodium intortum (Mill.) Urb.	17916
	18010
Desmodium scorpiurus (Sw.) Desv.	15419
Dolichos biflorus L.	13128
	14629
Dolichos falcatus Klein	15932
Dolichos gibbosus Thunb.	16359
Dolichos hosei Craib	12239
Dolichos lablab L.	
Dolichos species†	16053
	17557
Dolichos species†	16880–4
Glycine javanica L.	12600
	13300
	13420
	16417
	17185
	17673
Indigofera endecaphylla Jacq.	11412
	12240
	15362
Indigofera cryptantha Benth. ex Harv.	17084
Indigofera patens Eckl. & Zeh.	
Indigofera species†	16748
Lespedeza cuneata G. Don	16750

* Commonwealth Plant Introduction.

† Where the specific name is not given, identification of the species has not been completed.

TABLE 4 (*Continued*)

Species	C.P.I. Number*
Leucaena glauca (L.) Benth.	‡
Mucuna species†	17197
	17200-2
	17194
	17195
Pueraria phaseoloides (Roxb.) Benth.	11742
	12016
	15457
	16418
	16864
Pueraria thunbergiana (S. & Z.) Benth.	9363
Phaseolus aconitifolius Jacq.	14306
	14626-8
Phaseolus adenanthus G. W. F. Mey.	16070
Phaseolus bracteatus Nees & Mart.	11833
Phaseolus lathyroides L.	
Phaseolus trilobus Ait.	13758
Phaseolus species†	15739
	16367
Stylosanthes bojeri Vog.	10983
Stylosanthes gracilis H.B.K.	5630
	6058
	9215
Stylosanthes guianensis Sw.	15459
Stylosanthes juncea Micheli	11847
Stylosanthes species†	11494
	11496
Tephrosia species†	15461
Teramnus uncinatus Sw.	16680
Vigna nilotica (Delile) Hook. f.	16681
Vigna parviflora Welw.	16682
Vigna sinensis (L.) Endl. ex Haask	14307
Vigna vexillata (L.) Benth.	16683
Vigna species†	15541
	16684
Zornia diphylla (L.) Pers.	11501
	11855
	15469
	17216

* Commonwealth Plant Introduction.

† Where the specific name is not given, identification of the species has not been completed.

‡ Twelve introductions.

Leucaena glauca is a promising perennial browse shrub and none of the 518 plants grown at Strathpine has developed "little leaf". *Phaseolus lathyroides,* which is now an accepted pasture plant in Queensland, is highly resistant to the disease in the field, although infected plants are occasionally seen. In a plot of 2000 plants examined during the 1954-55 season six infected plants were found, but these soon died. Apparently the spread of the virus within areas of *P. lathyroides* is prevented by its lethal reaction following infection.

V. Discussion

The field and laboratory work on "little leaf" indicates that it is yet another strain of the virus complex which includes tomato "big bud", lucerne "witches' broom", and potato "purple top wilt". All of these, together with tobacco "yellow dwarf", have a common vector in *O. argentatus.* Laboratory studies which are in progress may clarify the relationships of these viruses.

A feature of interest is the apparent inability of laboratory-reared *O. argentatus* originally from the Canberra area to transmit "little leaf". This culture transmitted the other yellows viruses but is a relatively inefficient vector. It may be that the *O. argentatus* from Queensland is physiologically distinct and is adapted to the transmission of "little leaf" from indigenous and naturalized plants which are acting as reservoirs of the virus. Storey (1932) showed that the ability of a leafhopper to transmit a virus was inherited and the same phenomenon has been shown recently by Stubbs (1955) for the aphid vector *Myzus persicae* (Sulz.). The differential ability of *O. argentatus* from various areas to transmit virus strains of the "big bud–witches' broom" complex is an added complication and is being studied further.

One of the main objects of this work has been to assess the importance of "little leaf" as a factor limiting the establishment of recently introduced legumes in pastures. The work has shown that the problem is not as serious as first thought since some of the most promising legumes like *Indigofera endecaphylla* (C.P.I. 11412, 12240, and 15362), *Phaseolus lathyroides,* and *Leucaena glauca* possess a high degree of field resistance to the disease. Even with the promising *D. uncinatum* (C.P.I. 8990) spectacular symptoms are followed by apparent recovery during the height of the growing season. Although the important species lucerne and white clover become infected to some extent, symptoms are mild and the rate of spread of the virus within them is slow. On the other hand it seems that the establishment of *D. canum* and the glossy-leaved types of *D. uncinatum* may be prevented by "little leaf".

There is no evidence to suggest that natural selection of "little leaf"-resistant phenotypes is occurring in the established populations of the different susceptible introductions. Variation within them is at a low

"LITTLE LEAF" IN PASTURE LEGUMES

Fig. 1.—Healthy and "little leaf"-infected plants, similar in age, of *Crotalaria intermedia* (C.P.I. 1254).

Fig. 2.—Healthy and "little leaf"-infected plants, similar in age, of *Desmodium uncinatum* (C.P.I. 11740).

level because they are self-pollinated. As stated earlier, seed was sown from the few plants of *D. canum* and glossy-leaved *D. uncinatum* which had relatively mild virus symptoms and which survived infection in one experiment. The resultant progenies had no resistance to "little leaf". The pattern of susceptibility in the progenies of one of the earliest *D. uncinatum* introductions, C.P.I. 8990, has not altered over 6 years. The place of origin appears to be related to the resistance of strains in some species. In *I. endecaphylla* the South American and Indian types are highly resistant, whereas the African ones are susceptible.

VI. Acknowledgments

Thanks are due to Mr. J. F. Miles, Plant Introduction Officer, Division of Plant Industry, C.S.I.R.O., for permission to use his plots for the observations on the incidence of "little leaf". Mr. L. B. Beall collected much of the field data on the disease and Mrs. H. Morley assisted with the laboratory transmission work. Mr. S. T. Blake investigated the naming and authorities for the plant species mentioned in this paper.

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THE INFLUENCE OF SEED SIZE AND DEPTH OF SOWING ON PRE-EMERGENCE AND EARLY VEGETATIVE GROWTH OF SUBTERRANEAN CLOVER (*TRIFOLIUM SUBTERRANEUM* L.)

By J. N. Black*

(*Manuscript received October* 25, 1955)

Summary

Changes in the pre-emergence distribution of dry matter in subterranean clover (*Trifolium subterraneum* L.) variety Bacchus Marsh were followed at 21°C, using three sizes of seed and three depths of sowing, ½, 1¼, and 2 in. Decreasing seed size and increasing depth of sowing both reduce the weight of the cotyledons at emergence.

Seed of the three sizes were sown at three depths in pot culture at staggered intervals so that emergence was simultaneous. Dry weight in the early vegetative stage was proportional to seed size, and total leaf area and leaf numbers showed similar trends. Plants of each seed size grew at the same relative rate. No effect of depth of sowing could be detected, and this was shown to be due to the cotyledon area at emergence being constant for any given seed size, regardless of varying depth of sowing and hence of cotyledon weight.

It was concluded that seed size in a plant having epigeal germination and without endosperm is of importance: firstly, in limiting the maximum hypocotyl elongation and hence depth of sowing, and secondly, in determining cotyledon area. Cotyledon area in turn influences seedling growth, which is not affected by cotyledon weight. Once emergence has taken place, cotyledonary reserves are of no further significance in the growth of the plants.

I. Introduction

It has previously been shown (Black 1955) that both depth of sowing and temperature affect pre-emergence weight changes in subterranean clover, and that in particular there is a marked effect on the amount of dry matter remaining in the cotyledons at the time of emergence. It was postulated that the subsequent growth of the plants might be related to the extent of depletion of cotyledonary reserves, since in this species the cotyledons function not only as a storage organ in the seed but also as the first photosynthetic tissue. It is, however, possible to vary cotyledon weight on emergence not only by altering depth of sowing and temperature, but also by using seed of different sizes. It was accordingly decided to extend the scope of the investigation to include a range of seed sizes and, at least initially, to work at a pre-emergence temperature of 21°C, which has been shown to be optimal for hypocotyl elongation. The variety Bacchus Marsh has been used throughout these experiments.

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II. Methods

(*a*) *Classification of Seed by Size*

Following the examination of the range of seed size in a sample of seed which had been harvested and cleaned mechanically, it was decided to establish a series of size grades on a logarithmic basis. The smallest size was named size 1, the largest size 5, and the mean fresh weights of these grades are shown in Table 1.

The mean weight of seed of size 1 depends on the proportion of very small seeds, and has been found in practice to be slightly less than 3 mg. It should be noted that the seed had not been graded for commercial sale and therefore contained a large number of small seeds which would normally be rejected, at least for top-grade seed purposes; on the other hand, examination of hand-harvested material from the Waite Institute showed that even smaller seed does occur and will germinate under field conditions.

Table 1

SIZE-WEIGHT CLASSIFICATION OF SEED

Values as fresh weight per seed

Class :	1	2	3	4	5
Length of well-rounded seed (mm) :	1.7	2.1	2.3	3.6	3.0
Weight limits (mg) :	$\leqslant$3.49	3.50-4.49	4.50-5.59	5.60-7.09	7.10-8.89
Mean weight (mg) :	$<$3.0	4.1	5.0	6.4	8.0

A quantity of seed was then sorted by eye into the five classes, frequent checks being made on the efficiency of sorting by weighing individual seeds. Further, to prevent any possible overlap of the weights of seeds placed in each class, and to provide contrasting seed weights for experimental purposes, the even-numbered grades were rejected, and only sizes 1, 3, and 5 were retained.

(*b*) *Pre-emergence Weight Changes*

Seed of sizes 1, 3, and 5 was sown at depths of $\frac{1}{2}$, $1\frac{1}{4}$, and 2 in. in washed sand in 4-in. earthenware pots, which were held in a cabinet at a constant temperature of 21°C. Two pots of each of the three sizes from each depth of sowing were taken daily for sampling and three groups of 10 seeds removed from the sand in each pot. The seeds were separated into cotyledon, hypocotyl, and eventually root fractions, dried at 90°C for 24 hr, and each fraction weighed for the groups of 10 plants.

(*c*) *Early Vegetative Growth*

Seed of three sizes was incubated at 21°C for 24 hr so that hard seed might be rejected, and 15 germinated seeds were planted in washed sand in each standard 6-in. earthenware pot. The pots were kept before

emergence at an approximately constant temperature of 21°C and after emergence the seedlings were thinned down in two stages to eight per pot. Sowing dates were so adjusted that emergence of the seedlings of each size from each depth was simultaneous; the pots were then transferred to a plunge bed of moist shell grit, and arranged in four randomized blocks. Thus a mean value for each treatment was based on the data of a total of 32 plants. Before emergence, the pots were inoculated with a liquid culture of an effective strain of *Rhizobium trifolii*, and on subsequent inspection the plants were seen to be satisfactorily nodulated.

On emergence (February 8, 1955), and again about 2 weeks later, 1 g of a complete fertilizer mixture was added to each pot. The pots and the surrounding shell grit were watered at least daily and, despite the high rates of evaporation encountered during the summer months in Adelaide, no wilting was ever observed.

At each sampling occasion, the plants were cut off at ground level, and the tops separated into leaf and stem, the petioles being included in the stem fraction. The area of the leaves of one plant from each pot was determined by blue-printing and subsequent measurement with a planimeter; the leaf area per pot was then calculated from the area:weight ratio of the sample leaves and the total leaf weight for the pot. Roots were recovered by washing, firstly over a sieve and secondly in a dish, where any sand grains adhering to the roots could be removed. All plant material was dried for 24 hr at 90°C before weighing.

III. Results

(*a*) *Pre-emergence Weight Changes*

On any one daily sampling occasion, no differences could be detected in the weights of seedlings of the same seed-size grade sown at the three depths: germination was uniform, and the plants grew at the same rate.

Table 2

DISTRIBUTION OF DRY WEIGHT IN UNGERMINATED SEED

Size	Cotyledon Weight		Hypocotyl Weight		Testa Weight	
	(mg)	(%)	(mg)	(%)	(mg)	(%)
1	1.80	65	0.32	12	0.64	23
3	2.84	63	0.55	12	1.09	24
5	5.23	65	0.88	11	1.92	24

On emergence, daily determinations of weight were discontinued, and since the results are here presented as the mean plant weight for each seed size, regardless of depth of sowing, the mean weights for the last few days are derived from a decreasing total number of plants. Emergence was defined as the complete appearance of the cotyledons above

ground level, and since growth was very even no difficulty was experienced in deciding whether the plants had or had not emerged.

The distribution of weight in the original seed (means of 100 seeds of each size) is given in Table 2. It will be seen that in the mature seed there is no material difference in the proportions of cotyledon, hypocotyl, and testa.

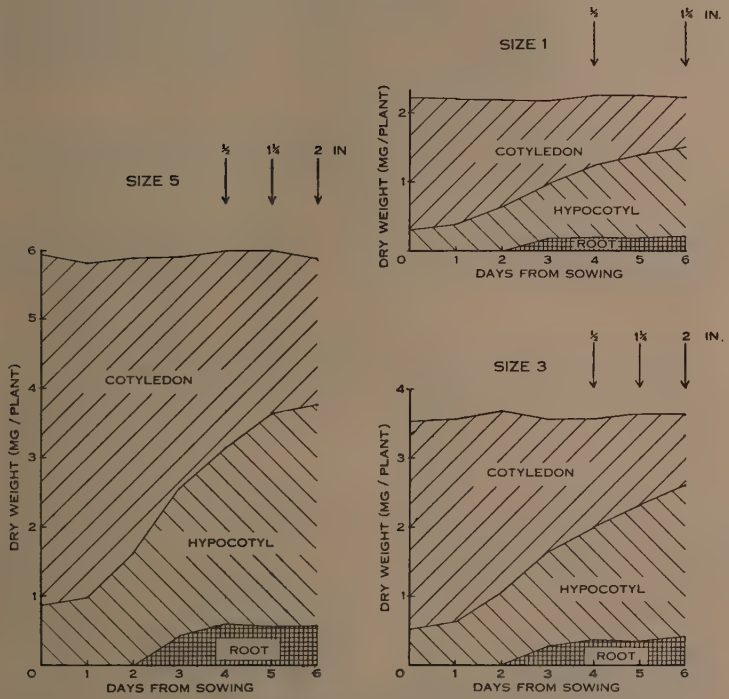

Fig. 1.—Changes in the pre-emergence distribution of dry weight for seed of sizes 1, 3, and 5.

The pre-emergence changes in the distribution of dry weight between cotyledon, hypocotyl, and, where necessary, root fractions for the three seed sizes are shown in Figure 1. The arrows above the total weight data indicate the day on which plants from that depth emerged. The pattern of weight change is clearly similar for all three sizes of seed, but while all sizes emerged from ½ in. on day 4, sizes 3 and 5 emerged from 1¼ in. on day 5 and size 1 on day 6. Sizes 3 and 5 both emerged from 2 in. on day 6, but it had been found in previous experiments that seed of size 1 was not capable of elongating to more than about 1½ in. and, in consequence, no sowing of size 1 seed was made at the 2 in. depth. The maximum hypocotyl elongation is discussed later.

It has, however, been noted (Black 1955) that the extent of reduction of cotyledonary reserves before emergence cannot be accurately measured by a technique involving rigid daily sampling, since emergence may have taken place at any time between the actual sampling occasions. The same restriction applies equally to the present data, and again it was considered desirable to plant a further series of pots which were sampled at the precise time of emergence. The cotyledon weight at emergence for the three seed sizes and the three depths of sowing (eight treatments altogether, since no emergence of size 1 seed from 2 in. depth could be expected), are given in Table 3. The effects of both seed size and depth of

TABLE 3

MEAN DRY WEIGHT OF COTYLEDONS ON EMERGENCE

Seed Size	Depth of Sowing:	Mean Dry Wt. (mg/plant)* at ½ In.	1¼ In.	2 In.
1		1.15	0.77	—
3		2.00	1.62	1.22
5		3.33	2.92	2.55
Min. significant differences:		At 5% level		0.160
		At 1% level		0.214
		At 0.1% level		0.281

* Weights ± 0.056 mg.

sowing were found on statistical analysis to be significant at the 0.1 per cent. probability level. By isolating the data so that complete two-way tables were available (i.e. all depths for sizes 3 and 5, and all sizes for depths ½ and 1¼ in.) it was possible to examine the depth of sowing × seed size interactions, which were found to be negligible.

(*b*) *Maximum Hypocotyl Elongation*

The failure of the small seed to emerge from 2 in. depth of sowing is of interest, and the maximum possible hypocotyl elongation of size 1 seed at 21°C was further examined. Seeds were planted with only a ½ in. covering of sand, and were allowed to grow on in complete darkness after emergence. Pots were removed at approximately 3-day intervals for determination of elongation and weight changes, and it is clear from Table 4 that when a length of 37 mm had been reached, at which time the cotyledon weight had been reduced to 0.53 mg, no further translocation from the cotyledons and no further elongation took place. Thus there is a maximum elongation of about 1½ in. in the virtual absence of a covering of sand or soil; while emergence from 1¼ in. through sand was found to occur readily, it is apparently close to the maximum depth from which emergence can take place for seed of this size. However, it may be expected that under field conditions the potential elongation may be reduced, to an

extent related to soil type and physical conditions. The maximum potential elongation of seed of sizes 3 and 5, determined in an identical manner, were 52 mm (about 2 in.) and 67 mm (about 2½ in.) respectively.

TABLE 4

HYPOCOTYL ELONGATION AND COTYLEDON WEIGHT (SIZE 1 SEED)

Days from Sowing:	0	3	6	9	13	24
Hypocotyl length (mm):	2.0	7.2	28.4	36.1	37.2	37.3
Cotyledon weight (mg):	1.80	1.22	0.72	0.53	0.52	0.53

(c) *Growth in the Early Vegetative Phase*

Plants from seed of sizes 1, 3, and 5 emerged from the three depths of sowing on February 8, 1955. Again, there were eight treatments only, since no seeds of size 1 were sown at 2 in. Pots were removed for sampling on three occasions at 10-day intervals, on February 18 and 28 and March 10; on each sampling occasion the weight of the plants and the constituent parts, leaf areas, and leaf numbers were obtained.

TABLE 5

PLANT WEIGHT AND LEAF AREA DATA

(*a*) *Log mean plant weight* (*mg*)

Size	1		3			5		
Depth of sowing (in.)	½	1½	½	1½	2	½	1½	2
Log mean wt. (± 0.0372) at:								
Harvest 1	0.896	0.842	1.186	1.185	1.166	1.363	1.405	1.377
Harvest 2	1.538	1.318	1.775	1.694	1.819	1.969	1.911	1.900
Harvest 3	1.870	1.788	2.213	2.138	2.163	2.360	2.270	2.309

Min. significant differences: At 5% level 0.106
At 1% level 0.142
At 0.1% level 0.185

(*b*) *Log mean leaf area* (cm^2)

Log mean area (± 0.0467) at:								
Harvest 1	$\bar{1}.981$	$\bar{1}.946$	0.172	0.226	0.182	0.339	0.411	0.383
Harvest 2	0.561	0.442	0.821	0.816	0.872	0.952	0.863	0.935
Harvest 3	0.805	0.809	1.217	1.133	1.210	1.351	1.248	1.317

Min. significant differences: At 5% level 0.133
At 1% level 0.178
At 0.1% level 0.233

The plant weight and leaf area data were analysed statistically after logarithmic transformation, and it was found that the effect of seed size on plant weight was positive and significant at the 0.1 per cent. probability level. Depth of sowing within each of the seed sizes was examined, and for plant weight was shown to be significant at the 5 per cent. level only for

seed of size 1, and not significant for sizes 3 and 5. The treatment × sampling occasion interaction was examined in each case but never reached significance. The relevant data, after transformation, are given in Table 5.

It will be seen that the significant seed size 1 × depth of sowing interaction on plant weight can be traced to the data for the second sampling occasion; there is no significant difference for either the first or third occasion. It is thought that this aberrant value may have been due

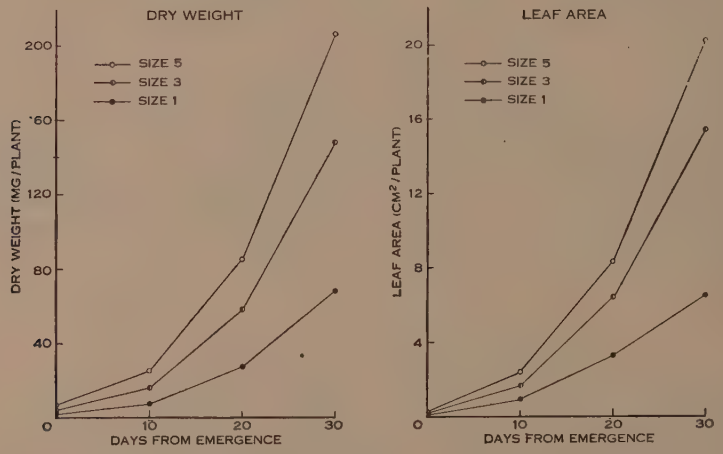

Fig. 2.—The influence of seed size on increase of dry weight and leaf area.

to slight inaccuracy in depth of planting, which would have a considerable effect when the depth is so close to the maximum potential hypocotyl elongation. The influence of seed size on leaf area was also positive and significant at the 0.1 per cent. level, and there were no significant effects of depth of sowing; nor did the treatment × sampling occasion interaction reach significance.

The plant weight and leaf area data (mean of all depths of sowing) for the three seed sizes are shown in Figure 2; the plant weight data shown for "0 days after emergence" have been added from the data outlined in Section III(*a*), since sowing procedure and temperature were immediately comparable. Leaf areas at emergence have also been added from separate data with identical seed size and environmental conditions.

It follows from the absence of an interaction between seed size and sampling occasion that the growth rate of plants grown from different initial seed sizes is identical; in which case an examination of the logarithms of the plant weight data should show that the trends of increasing weight between sampling occasions are parallel (Ashby 1932). The data are so presented in Figure 3; and since on inspection no departure

from parallelism can be observed, and in view of the absence of a seed size × sampling occasion interaction, it was not considered necessary to subject the parallelism to further statistical analysis.

The numbers of trifoliate leaves were counted on each sampling occasion, and the mean numbers per plant on the final occasion were 4.5, 6.4, and 8.0 for sizes 1, 3, and 5 respectively. There were no differences in leaf numbers between plants of the same seed size but from different depths of sowing.

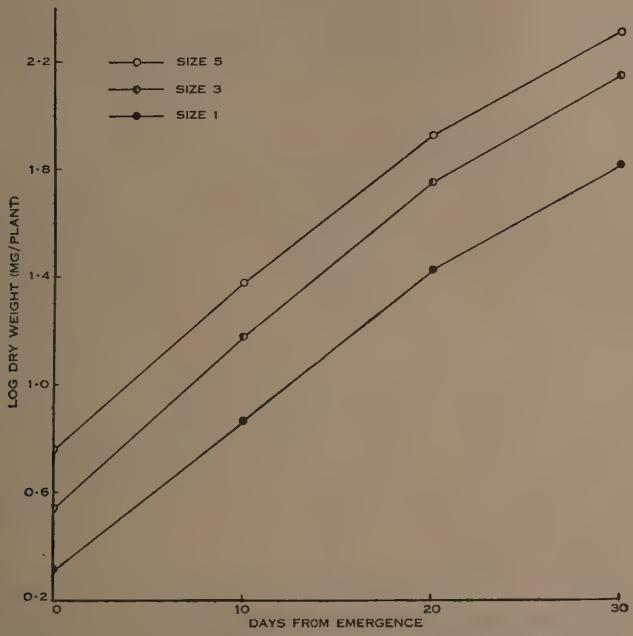

Fig. 3.—The influence of seed size on dry weight increase (logarithmic transformation).

The absence of any effect of depth of sowing on the dry weight or leaf area of the plants from any particular seed size—even at the sampling taken 10 days after emergence—was a most unexpected result in view of the marked differences in cotyledon weight at the time of emergence. Furthermore, no difference in the distribution of dry weight between leaf, stem, and root could be detected, even at the first sampling occasion, between plants of different seed size or from different depths of sowing. It had been suggested (Black 1955) that the reduction in cotyledon weight on emergence from deeper sowings might have adverse effects on subsequent growth by limiting the material available for the elaboration of the initial photosynthetic tissue, but this is not so. It has been shown that

while subsequent growth is directly related to variations in cotyledon weight caused by the choice of seed of different sizes, it is independent of variations in cotyledon weight caused by emergence from different depths of sowing. These apparently conflicting results could, however, be reconciled if the *area* of the cotyledons were dependent on seed size but were unaffected by depth of sowing, and if, as a result, cotyledon area were independent of reductions in cotyledon weight resulting from differences in depth of sowing. In this connexion, Blackman and Wilson (1954) have inferred from experiments in which plants were transferred between a number of shading treatments that the net assimilation rate of sunflower leaves is independent of variations in the ratio of leaf area to leaf weight; so that if, in the present experiments,

TABLE 6

AREA AND WEIGHT OF COTYLEDONS AT EMERGENCE

(*a*) *For size 5 seed*

Depth of Sowing (in.)	Mean Weight of Cotyledons (mg/plant)	Mean Area of Cotyledons (cm^2/plant)
½	3.30	0.164
1½	2.94	0.163
2	2.53	0.163

(*b*) *For ½ in. depth of sowing*

Seed Size	Mean Weight of Cotyledons (mg/plant)	Mean Area of Cotyledons (cm^2/plant)
1	1.18	0.078
3	2.10	0.118
5	3.30	0.164

emergence from different depths altered the *weight* of the cotyledons but not the *area*, then the plants would be expected to grow at the same rate, since both net assimilation rate—that is, dry weight increase per unit leaf area—and the area of the total leaf surface would be the same for plants emerging from different depths. The significance of seed size would then lie in a direct relationship between seed size and cotyledon area, so that a greater initial leaf area would be elaborated, resulting in a greater absolute dry weight increase.

A further series of pots were therefore planted with seed of size 5 at the three depths of sowing, and on emergence on July 25, 100 seedlings from each depth were taken for sampling. The cotyledons were removed for blue-printing and the weights of cotyledons and the remainder of the plants determined in groups of 10. The mean cotyledon area and cotyledon weight per plant are given in Table 6 and provide striking confirmation of the hypothesis put forward to account for the absence of an effect of depth

of sowing on subsequent growth. Cotyledon area remained constant despite a progressive reduction in cotyledon weight as depth of sowing increased. The areas and weights of cotyledons from plants of the three seed sizes from ½ in. depth of sowing are also given in Table 6.

IV. Discussion

It was previously suggested (Black 1955) that a reduction in cotyledon weight consequent upon increased translocation to the hypocotyl as depth of sowing increased might have lasting adverse effects on the subsequent growth of the plants, since less material would be available for the elaboration of the initial photosynthetic surface. In fact it has now been demonstrated that the weight *per se* of the cotyledons on emergence has no effect on seedling growth, and that this is due to the independence of cotyledon area and weight. A plant emerging from ½ in., as compared with one emerging from 2 in., has a higher cotyledon weight but an identical cotyledon area, and it has been shown that seedling growth depends directly on cotyledon area. Depth of sowing thus has no effect on subsequent growth, provided that a certain critical depth, determined by the size of seed size on the growth of pasture legumes. Fruwirth (1917; quoted by is simultaneous, plants from greater depths of sowing will be at a disadvantage as compared with those from shallower sowings since emergence will be progressively delayed as depth of sowing increases.

The influence of size of seed upon the subsequent growth and ultimate yield has been examined at various times for a number of species of economic importance. It is not proposed to attempt here an exhaustive review of these investigations; this was done by Kidd and West (1919), Kotowski (1926), and West (1930). The general conclusion to be drawn from these reviews and from more recently published data is that, in an annual plant, early growth is dependent on or even proportional to the size of seed. Only a few studies have, however, been made on the influence of seed size on the growth of pasture legumes. Fruwirth (1917; quoted by Kidd and West 1919), working with lucerne (*Medicago sativa* L.) and sainfoin (*Onobrychis sativa* Lam.), found that better crops were obtained by the use of larger seed, though with these perennial plants the initial advantage fails to persist. Findlay (1919) showed that within any one strain of red clover (*Trifolium pratense* L.) seed size was of importance, and Schmidt (1921), using crimson clover (*T. incarnatum* L.), also demonstrated that in the early stages of growth, production was markedly dependent on seed size.

The problem of seed size has also received attention in relation to heterosis, and it has been suggested by Ashby (1930) that early vigour can be related to embryo size rather than to differences in growth rate. These aspects have been reviewed by Whaley (1944) and Ashton (1946). In this connexion the seed of subterranean clover, with the exception of the testa, is clearly all "embryo", and since the proportion of testa in the total

seed weight is independent of seed size, embryo weight is directly related to seed weight. It is clear from the present data that the relative growth rates of the seedlings from different seed sizes are the same, and that, in agreement with Ashby's conclusions, the absolute growth of the plants depends upon embryo size. To use the analogy of Blackman (1919), plant weight at any one time depends on "initial capital", since "rate of interest" is the same. It is, however, possible to extend this analysis and to conclude that the importance of embryo size is to be found not so much in the *weight* of the tissue but in the *area* of the cotyledons contained therein, and that the weight of the plants at any one time, at least during the early vegetative phase, is a direct resultant of cotyledon area. It remains to be seen whether this effect persists, and if not, why not; investigations covering the whole growing period of the plant are in progress and will be reported in due course.

It also follows from a consideration of the significance of cotyledon area, and the failure to demonstrate an effect of residual cotyledon weight on subsequent growth, that seed reserves are of little or no importance in seedling growth once emergence has taken place, any reserve material remaining in the cotyledons being of no subsequent value to the plant.

It is accordingly possible to conclude that the importance of seed size in subterranean clover is twofold: firstly, seed size determines the depth from which emergence can take place, and secondly, seed size determines the initial area of the cotyledons. From the data here presented it is clear that the extent of transfer of cotyledonary material to the hypocotyl does not alter the area of the cotyledons on emergence and, assuming emergence can take place, it is the area of the cotyledons which determines the extent of the difference in the early vegetative growth stage between plants from different seed sizes. The same reasoning must not, however, be applied to plants of differing growth habit, but only those for which germination is epigeal and the whole of the seed consists of embryo and testa. Where germination is hypogeal, cotyledon area is obviously of no significance, and it may not in fact be possible to assume complete utilization of cotyledonary material in the subsequent growth of the seedling. The same holds for seeds in which a proportion of the weight is present as endosperm, whether germination be hypogeal or epigeal. Further it must be borne in mind that for some species there may be genetic differences within a population which affect seed size; this is unlikely to be extensive in autogamous species such as subterranean clover, where the whole range of seed sizes may be found on a single plant.

In conclusion it is suggested that the whole problem of seed size as it affects subsequent growth should receive further critical examination, particularly in relation to: (*a*) the nature of germination, whether hypogeal or epigeal; (*b*) the presence or absence of endosperm; (*c*) the maximum depth of sowing; (*d*) the potential cotyledon area.

V. Acknowledgments

The author wishes to thank Miss H. M. Uffindell for technical assistance, Professor C. M. Donald for his comments on the manuscript, and F. H. Brunning Pty. Ltd. for the supply of ungraded seed.

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EFFECTS OF A LOWLAND RICE CROP AND OF GYPSUM ON A SALINE ALKALI CLAY

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(*Manuscript received October* 19, 1955)

Summary

Lowland rice cropping for one season decreased the soluble salts, particularly the chlorides, in the top 30 in. of a saline alkali clay soil. The calcium:sodium ratio increased for soluble cations, but showed little change for exchangeable cations. The surface soil became slightly more water-stable, but below 3 in. the soil became easier to disperse. These changes had little effect on the growth of an irrigated annual pasture sown after rice cropping, except in the year of establishment. After 2 years' growth of the pasture, part of the soluble salts had returned to the top 30 in. of the soil.

The application of gypsum at 2 and 8 tons/acre before growing the lowland rice crop increased the calcium:sodium ratio of both soluble and exchangeable cations and reduced clay dispersion. Rice seedling establishment and yields of stubble-sown subterranean clover were higher on the gypsum-treated plots.

I. Introduction

The Wakool, Denimein, and Deniboota districts of southern New South Wales contain a large proportion of fine-textured saline alkali soils.‡ The irrigation water used has a conductivity less than 250 micromhos/cm, and when the soils are irrigated the electrolyte concentration falls, at least temporarily, below the level needed to maintain flocculation.

On certain of these soils rice is grown for a single season as a soil-conditioning crop before the establishment of irrigated pastures. The root growth of the crop is popularly credited with the power of "opening up" the topsoil. The first part of this experiment was designed to determine the effects of a single rice crop on the physico-chemical properties of a commonly occurring saline alkali clay soil, and on the productivity of a stubble-sown pasture. The soil studied does not contain any reserve of lime or gypsum in the top 2 ft, and its permeability at high moisture contents is very low. Under these conditions the most suitable method of amelioration may be the application of gypsum followed by intensive leaching. After removal of excess exchangeable sodium, soil structure may be improved by

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‡ "Saline-alkali soils are defined as those with a conductivity of the saturation extract greater than 4 millimhos/cm at 25°C and more than 15 per cent. of the exchange complex saturated with sodium" (U.S. Dep. Agric., Agric. Hbook. No. 60 (1954)).

a period of pasture ley. The second part of the experiment was designed to determine the effectiveness of these methods of amelioration.

II. Soil Type

The experiment was laid down on Riverina clay at the Falkiner Memorial Field Station near Deniliquin, N.S.W.

A description of the soil profile* follows:

Horizon	Depth	Description
A	0-1 in.	Brownish light grey silty clay loam (20% clay, 25% silt). Moderate grade of platy structure (¼ in.), hard and brittle when dry. Sudden change, but with stringers of A horizon running into B horizon. Thickness varies from nil to 2 in. owing to slight crabholey relief.
B	1-17 in.	Brownish dark grey heavy clay (62% clay). When the material is dry the structure is a strong grade of angular blocky, fine (½ in.) above but becoming very coarse (8 in.) below. When wet the material appears structureless. The consistence is very hard when dry, firm and plastic when wet. A gradual change over 4 in. to B_{ca} horizon.
B_{ca}	17-33 in.	Dull brown-grey medium clay (66% clay) with a trace of lime. When dry the material is very coarse (8 in.) angular blocky, and very hard. When wet it is structureless and plastic. A gradual change to B_{ca}-C horizon.
B_{ca}-C	33-100 in.	Grey and yellow-grey, mottled with black and brown flecking, medium clay (59% clay), with light crystalline gypsum (1%). Lime appears in the upper part of this horizon but disappears at 41 in. depth. The material is similar in structure and consistence to the B_{ca} horizon.

The clay of the B horizon is essentially illitic. There is no water-table within 20 ft of the surface.

III. Techniques

(*a*) *Sampling*

Samples for chemical analysis and macro-organic matter determination were taken with a 1-in. diameter Veihmeyer tube, six cores per plot being bulked for each of the depths 0-3 in., 3-12 in., 12-21 in., and 21-30 in. Samples for other physical analyses were taken at two points per plot with a Coile core sampler of 4 in. diameter.

(*b*) *Chemical Analyses*

The methods employed for determination of pH, anions, and nitrogen, and for the extraction of soluble and exchangeable cations, were essentially those described by Piper (1942). In the leachates, sodium and potassium were determined spectrochemically using either the Lundegårdh air-acetylene flame technique or the "EEL" flame photometer, and calcium

* Supplied by B. E. Butler, Division of Soils, C.S.I.R.O., Canberra.

and magnesium by the Lundegårdh flame or by titrations with the disodium salt of ethylene diamine tetra-acetic acid. Owing to the presence of gypsum, which is not soluble in 40 per cent. aqueous alcohol, it was necessary to correct the values for calcium in certain samples. The ammonium chloride leachings were analysed for sulphate ions, and the amount of calcium equivalent to the sulphate found was deducted from the exchangeable calcium and added to the soluble calcium. Nitrate produced during incubation of samples in a humid atmosphere at 25°C was determined by the brucine method of Peech and English (1944). Free iron oxides were extracted by the method of Jeffries as modified by Williams (1950). The phosphate and nitrate contents of diffusion extracts of leaves and stems were determined by the methods of Plant, Jones, and Nicholas (1944).

(*c*) *Physical Analyses*

Macro-organic matter was separated by the method of Barley (1955). The percentage dispersion ($100S/D$) was measured at the 0.2 mm diameter limit. S is the percentage of the total mass made up of particles of less than the specified diameter after mild dispersion. D is the percentage with less than the specified diameter as determined by the usual particle size analysis. Mild dispersion was effected by the following method. Soils were first air-dried and broken by hand to pass a 1-cm sieve. Sieved samples were wet under 2 cm tension for 48 hr, and were then shaken end over end at 16 r.p.m. for 5 min in 5-oz bottles half filled with irrigation water. Particles exceeding 0.2 mm in diameter were separated by wet sieving. The apparent density of 4-in. diameter cores was measured with the sampler described by Coile (1936). Regression equations relating apparent density and moisture content were established for each depth, and were used to bring values to a common moisture content. The apparent density of air-dry clods of 20-40 g weight was determined by a paraffin-coating and immersion method.

IV. Effects of Rice Cropping

(*a*) *Treatments*

The following treatments were imposed:

(i) Dry fallow: cultivated and graded on September 25, 1950;

(ii) Flood fallow:* as for (i), then inundated from December 22, 1950, until March 7, 1951;

(iii) Rice crop:* as for (ii), but cropped with Caloro rice.†

The treatments were replicated in six randomized blocks. Plots were 14 ft square and their boundaries were not less than 18 ft apart. Soil sampling

* (ii) and (iii) are together referred to as inundation treatments.

† Dry weight of rice tops at maturity, 9550 lb/acre. Plant density at maturity, 8.4 plants/sq. link.

sites were confined to an area 8 ft square centred within each plot. All plots were top-dressed with sulphate of ammonia at 1.0 cwt/acre on December 20, 1950, and again on February 15, 1951.

On April 26, 1951, the plots were disc-cultivated, the rice tops on treatment (iii) being partly incorporated, and on May 11, 1951, they were sown with Bacchus Marsh subterranean clover (*Trifolium subterraneum* L.) and Wimmera ryegrass (*Lolium rigidum* Gaud.). Clover seed was inoculated with *Rhizobium* before sowing. The pasture plots were top-dressed with monocalcic phosphate at 0.8 cwt/acre on May 17, 1951, on March 14, 1952, and in the autumn of subsequent years. Flood irrigations were given on October 20, 1951, and on March 25, April 1, and October 1, 1952, and in the autumn and spring of subsequent years. At the end of each growing season the plots were grazed by sheep.

Complete sets of soil samples were collected between April 6 and 16, 1951, and between April 20 and 30, 1953. Water samples were collected from the head ditch during irrigation in October 1952.

(*b*) *Results*

(i) *Chemical Analyses.* (1) *Ionic Composition of Irrigation Water.*— The water used for irrigation at the experimental station is obtained from the River Murray by diversion at Yarrawonga Weir. At Yarrawonga the water contains about equal amounts of sodium, calcium, and magnesium

TABLE 1

IONIC COMPOSITION OF IRRIGATION WATER (M-EQUIV./LITRE)

Ion	River Murray at Yarrawonga*	Head Ditch at Experimental Site
Ca	0.18	0.25
Mg	0.21	0.32
K	0.29	0.08
Na		0.82
Cl	0.18	0.31
HCO_3	0.34	0.94
SO_4	0.08	0.14

* Average of 11 samples collected over 6 years; results kindly made available by State Rivers and Water Supply Commission of Victoria.

(each 0.2 m-equiv./l). After the water has travelled 70 miles in open earth channels to the experimental site, sodium has increased to 0.8 m-equiv./l. This increase is partly due to evaporation, as is shown by the increase in chloride and sulphate ions; but the greater part of the added sodium must have come from the soil of the irrigation channels and ditches. The ionic composition of the water is given in Table 1.

TABLE 2

EFFECTS OF INUNDATION TREATMENTS ON SOIL CHLORIDES AND CATIONS (M-EQUIV./100 G) AND pH

Depth:	0-3 Inches			3-12 Inches			12-21 Inches			21-30 Inches		
Treatment:*	(i)	(ii)	(iii)	(i)	(ii)	(iii)	(i)	(ii)	(iii)	(i)	(ii)	(iii)
April 1951												
Chloride	0.4	0.1	0.2	1.5	0.1	0.2	3.1	0.5	1.0	5.2	1.5	2.3
Soluble Ca	0.3	0.5	0.4	0.1	0.4	0.3	0.1	0.8	n.d.	6.6	3.9	3.8
Soluble Na	0.7	0.3	0.4	1.8	0.3	0.3	3.1	0.9	n.d.	5.3	2.4	3.2
Exchangeable Ca	6.9	7.0	6.3	8.9	7.9	7.7	8.8	7.6	n.d.	6.9	7.1	7.2
Exchangeable Na	2.3	1.6	1.5	5.0	3.6	4.2	6.7	6.6	n.d.	7.3	8.5	8.2
pH (1:5 suspension)	7.2	7.3	7.3	7.8	8.0	8.2	8.2	8.7	8.6	7.9	8.3	8.2
April 1953												
Chloride	0.7	0.4	0.5	1.0	0.5	0.6	3.0	1.2	1.6	6.8	2.0	3.2
Soluble Ca	0.5	n.d.	0.4	0.4	n.d.	0.3	0.6	n.d.	0.5	9.2	n.d.	7.7
Soluble Na	0.6	n.d.	0.6	0.8	n.d.	0.6	2.7	n.d.	1.6	5.6	n.d.	3.0
Exchangeable Ca	7.0	n.d.	7.5	9.2	n.d.	8.5	9.3	n.d.	8.3	7.0	n.d.	7.9
Exchangeable Na	1.7	n.d.	1.8	3.3	n.d.	3.7	7.5	n.d.	7.4	8.0	n.d.	7.7
pH (1:5 suspension)	7.0	7.1	7.1	8.0	8.1	7.9	8.5	8.2	8.3	7.9	8.0	7.8

* (i) Dry fallow; (ii) flood fallow; (iii) rice crop.

(2) *Chloride, Cations, and pH.*—During inundation the greater part of the chloride was leached from the 0-30 in. depth of soil; but appreciable return movement towards the surface occurred under the irrigated annual pasture (see Table 2). Additional data on chloride movement were obtained by following concentration changes to a depth of 9 ft on a plot 16 by 26 ft located on Riverina clay near the experimental area. Samples were taken on November 26, 1951, 10 days before flood fallowing, on March

TABLE 3

EFFECTS OF FLOOD FALLOW AND SEASON* ON DISTRIBUTION OF CHLORIDE
Plots flood-fallowed from 6.xii.1951 to 7.iii.1952

Depth (ft)	Soil Chloride (m-equiv./100 g) at			
	26.xi.1951	11.iii.1952	10.ix.1952	26.iii.1953
0-3	4.0	3.2	2.7	3.3
3-6	6.2	6.2	6.6	7.3
6-9	6.5	6.3	6.5	6.8
0-9	5.5	5.3	5.2	5.8

* For period 12.iii.1952-10.ix.1952, rainfall was 8.9 in., evaporimeter total 16.5 in.; for period 11.ix.1952-26.iii.1953, rainfall was 10.3 in., evaporimeter total 47.0 in.

7, 1952, 4 days after flood fallowing, and also on September 10, 1952, and March 26, 1953. The plot was kept free of vegetation throughout the period of study. The chloride contents at each date are given in Table 3. Since some lateral movement of water occurred, chloride reduction at one depth need not be completely balanced by gain at some lower depth. The data reveal considerable loss of chloride from the top 3 ft during inundation, further displacement downwards by winter rains, and a definite increase in chloride at all depths during the period of dry summer fallow.

Inundation increased soluble calcium and decreased soluble and exchangeable sodium from 0 to 21 in. depth. The initial pH level was highest at 12-21 in. where the ratio of soluble calcium to soluble sodium was least. Inundation increased the pH at each depth, the increase being largest where most chloride was removed. Differences between treatments were reduced after 2 years' irrigation of annual pasture. Data are given in Table 2.

(3) *Free Iron Oxides.*—A marked local redistribution of free iron oxides occurred during inundation. Bleached pockets contrasted with sites of iron accumulation in the top ½ in. of soil, along rice root channels and on cleavage faces. No consistent difference was found between the free iron oxide concentration in water-stable aggregates and in total soils.

(4) *Nitrogen.*—Neither flood fallowing nor rice cropping changed the total nitrogen content of the soil, despite the accumulation of 110 lb/acre of nitrogen in the rice tops. When soil samples taken in September 1951 were incubated, least nitrate was found where rice tops had been incorporated. After 2 years' growth of pasture the nitrogen content of the soil had increased and had become fairly uniform on all treatments.

(ii) *Physical Analyses.* (1) *Macro-organic Matter.*—Although 3400 lb/acre of oven-dry roots was produced by the rice crop, this amount of macro-organic matter was almost balanced by breakdown of plant residues during the period of inundation. Net addition of macro-organic matter by rice roots amounted to 700 lb/acre. Thirty-six per cent. by weight of rice roots occurred in the top 3 in. of soil, and few roots extended deeper

TABLE 4

EFFECTS OF INUNDATION TREATMENTS ON PERCENTAGE DISPERSION (0.2 MM LIMIT)

Samples taken in April 1951

Treatment	Percentage Dispersion at			
	0-3 In.	3-12 In.	12-21 In.	21-30 In.
Dry fallow	60	76	90	76
Flood fallow	57	77	100	96
Rice crop	59	85	98	100

than 20 in. The incorporation of rice tops added 9000 lb/acre of macro-organic matter. After 2 years about one-quarter of the weight of this material could still be recovered as macro-organic matter. Two years' pasture growth increased the amount of macro-organic matter present in the soil by 6000 lb/acre, most of the material being added to the top 3 in.

(2) *Percentage Dispersion.*—Table 4 shows that inundation made the soil below 3 in. easier to disperse, but little change was observed in the top 3 in. Some difference was, however, noticed in the field. During the first season of pasture growth, the surface of the summer-inundated plots remained mealy and friable under the action of winter rains whereas the surface of dry-fallowed plots slaked down.* Differences in the water stability of the surface soil were less evident in the second season of pasture growth and were not detectable by April 1953.

(3) *Apparent Density.*—The treatments had no effect on the apparent density of clods of 20-40 g weight separated from the top 3 in. of soil. Measurements of the apparent density of core samples showed that the layer disturbed by cultivation and grading consolidated during inundation. After 2 years' growth of irrigated pasture the treatments did not significantly differ in apparent density.

* For plates showing the difference in physical condition of the surface, see *J. Aust. Inst. Agric. Sci.* 19: 99-105 (1953).

(iii) *Pasture Establishment, Growth, and Yield.*—On May 11, 1951, all plots were sown with a mixture of subterranean clover (5 lb/acre) and Wimmera ryegrass (6 lb/acre). Brairding began on May 19 following 0.30 in. of rain on May 14 to 15, but some seedlings stalled before further rain fell on May 24, when 0.90 in. was received. Most stalling occurred on the dry-fallowed plots. Fewer clover plants became established on the rice-cropped treatment than on the flood-fallowed, because of the cloddy condition of the cropped plots after cultivation. The rounded clover seeds tended to fall between and become buried by clods more readily than the light, long grass seeds, which were retained by minor surface irregularities. On a few patches where large clods were absent, clover establishment was

TABLE 5

ESTABLISHMENT, DENSITY, AND YIELD OF IRRIGATED PASTURE IN THE FIRST SEASON FOLLOWING INUNDATION TREATMENTS

Treatment	Plant Establishment (% viable seeds)		Density (plants/4 sq. lk.)		Dry Matter Yield (cwt/acre)		
	Ryegrass	Clover	Ryegrass	Clover	Ryegrass	Clover	Weeds
Dry fallow	6.9	19.4	3.6	1.6	12.7	0.8	3.7
Flood fallow	37.3	28.9	18.4	2.4	34.9	0.3	0.1
Rice crop	30.3	15.1	15.2	1.3	25.1	0.1	0.0
Min. sig. diff. ($P = 0.05$)	7.6	10.4	3.8	0.9	6.4	0.6	—

similar to that found on flood fallow. The percentage establishment and density of each species are given in Table 5.

In early September 1951 ryegrass on the rice-cropped treatment appeared more yellow than ryegrass on other treatments. A diphenylamine test for nitrate made at this time showed an absence of nitrate in ryegrass stems from the cropped treatment, traces present for the flood fallow, and greater amounts for the dry fallow. Ryegrass and subterranean clover wilted more rapidly on the dry fallow than on the inundation treatments before and after irrigation in October 1951. Dry matter yields determined by quadrat sampling on October 2, 1951, are shown in Table 5. In 1952 the aspect of the pasture changed to clover dominance, ryegrass showing symptoms of nitrogen deficiency on the rice-cropped treatment in autumn and on all treatments in spring. Dry matter yields determined on November 4, 1952, did not differ between the treatments. The mean yield of ryegrass was 20 cwt/acre and of clover 47 cwt/acre. The treatments did not noticeably differ in yield of either species in 1953 or in 1954.

(*c*) *Discussion*

The inundation treatments, which leached more than half the chloride from the top 30 in. of Riverina clay, proved more effective in reducing

salinity than has the intermittent irrigation of pasture. Two years' irrigation of annual subterranean-clover–Wimmera-ryegrass pasture, sown on dry-fallowed plots, failed to remove chloride from the top 30 in. of soil. Five years' irrigation of perennial Rhodes grass (*Chloris gayana* Kunth) pasture, grown on Riverina clay in plots of similar size to those studied in the inundation experiment, removed only one-sixth of the chloride from the top 18 in. of soil.

The extent of the increase in calcium: sodium ratio caused by inundation was not sufficient to compensate for reduction in salinity and did not prevent some dispersion of the saline alkali clay studied. In the top 3 in. of soil other factors operated to reduce dispersion. Particle binding may have been chiefly caused by microbial growth on plant remains during inundation, and, in the case of the cropped treatment, by a conspicuous growth of mycelium on the incorporated rice tops. Accumulation of ferric compounds along root channels and cleavages has been suggested as a cause of water stability in soil treated by inundation and drying (Barley 1953); but no consistent difference was found between the free iron oxide content of water-stable aggregates and that of total soil. Moreover, rusty mottles were well developed not only in the top 3 in. of soil but also at lower depths, where considerable dispersion occurred.

Removal of nitrogen by the rice crop did not cause a corresponding decrease in the nitrogen content of the soil. Willis and Green (1948) previously found that losses of volatile nitrogen compounds during inundation were reduced in the presence of the crop, and that increases in total nitrogen sometimes occurred owing to fixation.

Hallsworth, Lemerle, and Rayner (1952) studied the effect of rice growing on soils of the Murrumbidgee Irrigation Areas. These soils were less saline, contained less exchangeable sodium, and were of lower pH than Riverina clay. Rice growing on these soils decreased pH and salinity. Hallsworth, Lemerle, and Rayner concluded that chloride did not tend to increase to its former levels within 10 years after the cessation of rice cropping. On Riverina clay an appreciable increase in soluble chloride and sodium concentration occurred when inundation was followed by intermittent irrigation of pastures. The amount of chloride and sodium added in the irrigation water was not sufficient to account for this increase, and most of the salt must have been derived from the deeper parts of the profile.

Effects of flood fallow or rice cropping on the herbage production of the sown pasture were not important after the first growing season. Flood fallow improved pasture establishment in the first season, chiefly by increasing water supply. Increased water stability of the surface after inundation had little effect on brairding, which was completed before sufficient rain fell to slake the surface of controls. Ryegrass dominated the pasture in its first year, when yields were limited by low plant density on dry fallow, and by nitrogen deficiency where rice tops had been

incorporated. In the subsequent seasons of clover dominance herbage yields did not respond to treatment differences in salinity or dispersion.

V. Effects of Gypsum Application Followed by Rice Cropping

(*a*) *Treatments*

After cultivation and grading of the experimental area, 200 mesh gypsum was applied by hand-spreading at the rate of 2 and 8 tons/acre. The treatments were replicated in 12 adjacent blocks. Plot size was 16 by 11 ft. Caloro rice seed was broadcast at 130 lb/acre over the entire area, and plots were then scarified to a depth of 1-2 in. The trial was irrigated as one unit for the first time on November 16, and then at 3-day intervals. Inundation began on December 22, 1950, and ceased on March 7, 1951. All plots were top-dressed with ammonium sulphate at 1.0 cwt/acre on December 20, 1950, and again on February 15, 1951.

After drainage and soil sampling the top growth of the mature rice crop was removed from six of the 12 blocks. The entire area was then disc-cultivated, the rice tops on the remaining six blocks being partly incorporated, and on May 11, 1951, the plots were sown with Bacchus Marsh subterranean clover and Wimmera ryegrass. Clover seed was inoculated with *Rhizobium* before sowing. The pasture plots were top-dressed with monocalcic phosphate at 0.8 cwt/acre in May 1951 after soil sampling and in the autumn of subsequent years. In March 1952, plots which had been treated with gypsum in 1950 were top-dressed with gypsum at 5 cwt/acre. Flood irrigations were given on October 20, 1951, and on March 25, April 1, and October 7, 1952, and in the autumn and spring of subsequent years. The plots were grazed by sheep at the end of the 1951, 1952, and 1953 growing seasons, and in June and October 1954.

Complete sets of soil samples were collected between April 12 and 18, 1951, and between May 4 and 29, 1953. Water samples were collected from the head ditch during irrigation on October 7, 1952.

(*b*) *Results*

(i) *Chemical Analyses.* (1) *Chloride, Cations, and pH.*—Gypsum treatments greatly increased the loss of chloride during inundation. Adding gypsum at 2 tons/acre is equivalent to adding 6 m-equiv. of calcium per 100 g of soil over a depth of 3 in. It can be seen from Table 6 that 50 per cent. of the calcium added at this rate was retained in the 0-3 in. layer as exchangeable calcium. Where gypsum was added at 8 tons/acre, 12 per cent. of the calcium added remained in the 0-3 in. layer as gypsum, and 25 per cent. as exchangeable calcium. The pH decreased where gypsum had been applied, the decrease extending to 12 in. depth at the higher rate of application. Two years of pasture produced little change in either the pH or the exchangeable cations, but there was some return of soluble sodium and chloride ions to the upper foot of the profile. Quantitative data are given in Table 6.

TABLE 6

EFFECTS OF INUNDATION, WITH AND WITHOUT GYPSUM ADDED TO THE SOIL, ON CHLORIDE AND CATIONS (M-EQUIV./100 G) AND pH

Depth:	0-3 Inches				3-12 Inches				12-21 Inches				21-30 Inches			
Treatment:*	(a)	(0)	(2)	(8)	(a)	(0)	(2)	(8)	(a)	(0)	(2)	(8)	(a)	(0)	(2)	(8)
April 1951																
Chloride	0.4	0.2	0.1	0.1	1.5	0.2	0.1	0.1	3.1	0.5	0.2	0.3	5.2	1.3	0.5	0.1
Soluble Ca	0.3	0.3	0.3	3.4	0.1	0.5	0.4	1.0	0.1	0.7	0.8	n.d.	6.6	6.2	6.5	3.0
Soluble Na	0.7	0.3	0.2	0.2	1.8	0.3	0.2	0.5	3.1	0.8	0.6	n.d.	5.3	2.7	2.3	1.3
Exchangeable Ca	6.9	6.7	9.8	12.9	8.9	7.8	8.0	7.6	8.8	7.3	7.7	n.d.	6.9	6.6	7.3	7.4
Exchangeable Na	2.3	1.7	0.8	0.6	5.0	4.1	3.5	2.7	6.7	7.7	8.3	n.d.	7.3	9.3	9.4	7.9
pH (1:5 suspension)	7.2	7.2	6.8	6.6	7.8	8.0	7.9	7.6	8.2	8.7	8.7	8.6	7.9	8.1	8.2	8.3
May 1953																
Chloride	0.7	0.4	0.4	0.3	1.0	0.5	0.3	0.2	3.0	1.4	0.8	0.5	6.8	2.3	1.2	0.5
Soluble Ca	0.5	0.4	0.7	1.8	0.4	0.3	0.3	n.d.	0.6	0.5	0.6	n.d.	9.2	7.7	6.6	5.6
Soluble Na	0.6	0.6	0.5	0.5	0.8	0.6	0.5	n.d.	2.7	1.6	1.1	n.d.	5.6	3.0	2.6	2.0
Exchangeable Ca	7.0	7.5	9.8	14.3	9.2	8.5	8.9	n.d.	9.3	8.3	7.8	n.d.	7.0	7.9	7.5	6.0
Exchangeable Na	1.7	1.8	1.0	0.6	3.3	3.7	3.1	n.d.	7.5	7.4	7.1	n.d.	8.0	7.7	8.0	7.8
pH (1:5 suspension)	7.1	7.0	6.8	6.6	7.9	7.9	7.8	7.5	8.3	8.5	8.6	8.5	7.8	7.9	7.9	8.1

* (a) Adjacent land, neither treated with gypsum nor inundated. (0) Inundated without addition of gypsum. (2) Inundated after addition of gypsum at 2 tons/acre. (8) Inundated after addition of gypsum at 8 tons/acre.

(2) *Total Nitrogen.*—The gypsum treatments did not affect the amount of total nitrogen present after inundation. Two years' growth of pasture increased the nitrogen content of the top 3 in. of soil by 10-15 mg/100 g on all treatments. At 3-12 in. depth, the nitrogen content increased by 20 mg/100 g where gypsum had been applied at 8 tons/acre, but showed little change on other treatments.

TABLE 7

EFFECTS OF INUNDATION, WITH AND WITHOUT GYPSUM ADDED TO THE SOIL, AND OF SUBSEQUENT PASTURE GROWTH ON MACRO-ORGANIC MATTER

Treatment	Added Gypsum (tons/ac)	Macro-organic Matter in Soil (g/100 g) in			
		April 1951		May 1953	
		At 0-3 In.	At 3-12 In.	At 0-3 In.	At 3-12 In.
Not inundated	0	0.25	0.11	0.61	0.17
Inundated	0	0.37	0.14	0.93	0.13
	2	0.38	0.10	0.57	0.12
	8	0.41	0.13	0.62	0.15
Min. sig. diff. between inundated treatments ($P = 0.05$)		N.S.	N.S.	0.09	0.02

(ii) *Physical Analyses.* (1) *Macro-organic Matter.*—The amount of macro-organic matter present in the soil after rice growing did not differ between the gypsum treatments. In April 1953, after two seasons' pasture growth, less macro-organic matter was present at 0-3 in. depth where gypsum had been applied. However, at 3-12 in. depth more macro-organic matter was present where gypsum had been applied at 8 tons/acre than on other treatments. Data are given in Table 7.

(2) *Percentage Dispersion.*—After being irrigated in late November 1950 the gypsum-treated plots remained mealy and moist at the surface. A crust of dispersed clay formed on nil plots. This crust dried and cracked very rapidly. Gypsum reduced dispersion to a depth of 3 in. where applied at 2 tons/acre, and to a depth of 12 in. where applied at 8 tons/acre. The treatments did not prevent inundation from dispersing the soil at lower depths. Data are given in Table 8. The incorporation of rice tops reduced dispersion of the top inch of soil during the first season of pasture, but the effect did not persist through the second season.

(3) *Apparent Density.*—Less consolidation of the cultivated layer occurred during inundation where gypsum had been applied. Moreover, the apparent density of gypsum-treated soils was greatly reduced by 2 years' growth of pasture. Incorporation of rice tops, compared with their removal, at first reduced the apparent density of the top 3 in. of soil; but after 2 years' pasture, core or clod density did not differ between the

stubble treatments. The apparent densities of core samples of 4 in. diameter, and of clods of 20-40 g weight, are recorded in Table 9.

(iii) *Performance of the Rice Crop.*—Brairding began on gypsum-treated plots on November 27, 1950, 11 days after the first irrigation. An even stand of seedlings developed within a few days. The first seedlings

TABLE 8

EFFECTS OF INUNDATION, WITH AND WITHOUT GYPSUM ADDED TO THE SOIL, ON PERCENTAGE DISPERSION (0.2 MM LIMIT)

Samples taken in April 1951

Treatment	Added Gypsum (tons/ac)	Percentage Dispersion at			
		0-3 In.	3-12 In.	12-21 In.	21-30 In.
Not inundated	0	60	76	90	76
Inundated	0	60	83	99	93
	2	52	83	100	93
	8	51	57	100	95

appeared on nil plots 15 days after the first irrigation. Counts taken when brairding was finished are recorded in Table 10. On December 14, rice seedlings began to show yellow tipping of the leaves, the incidence being greater on the gypsum-treated plots. Analyses of diffusion extracts of

TABLE 9

EFFECTS OF INUNDATION, WITH AND WITHOUT GYPSUM ADDED TO THE SOIL, ON APPARENT DENSITY

Treatment	Added Gypsum (tons/ac)	Apparent Density (g/c.c.) in			
		April 1951	May 1953		
		0-3 In. Cores	0-3 In. Cores	3-6 In. Cores	0-3 In. Clods
Not inundated	0	1.22	1.33	1.34	1.51
Inundated	0	1.33	1.32	1.41	1.63
	2	1.31	1.24	1.36	1.54
	8	1.26	1.18	1.31	1.46
Min. sig. diff. between inundated treatments ($P = 0.05$)		0.04	0.05	0.06	0.06

seedling leaves showed lower phosphate concentration in extracts of leaves taken from gypsum plots than from controls. Nitrate was not present in any detectable concentration. The plants showed no response to spot applications of either ammonium sulphate or monocalcic phosphate or both. The density and yield of the rice crop at maturity are given in Table 10.

(iv) *Pasture Growth.*—On May 11, 1951, all plots were sown with a mixture of subterranean clover (5 lb/acre) and Wimmera ryegrass (6 lb/acre). After 0.30 in. of rain from May 14 to 15 no further rain fell until May 24, when 0.90 in. was received. Germination began on May 17, and some seedlings stalled between this date and May 24. Establishment did not differ between the gypsum treatments. Where rice tops had been removed, cultivation produced a more even seed bed and establishment of the clover was increased by 50 per cent. Ryegrass dominated the pastures in winter and spring, and final yield did not differ between the various treatments. Mean dry matter yield equalled 0.5 cwt/acre of clover and 38 cwt/acre of ryegrass. Analyses of diffusion extracts of clover leaves and ryegrass stems collected in September did not show any difference in phosphate concentration between gypsum treatments and controls.

TABLE 10

DENSITY AND YIELD OF THE RICE CROP

Treatment	Density (plants/sq. lk.)		Dry Weight of Tops at Maturity	
	Seedling Stage	Maturity	(g/plant)	(cwt/acre)
Gypsum (tons/acre): 0	8.5	8.5	5.2	87
2	12.1	10.1	4.6	92
8	13.4	11.3	4.2	94
Min. sig. diff. ($P = 0.05$)	3.2	1.2	0.7	—

In 1952 the aspect of the pasture changed to clover dominance. Ryegrass plants, although numerous, were dwarfed and yellow. Clover burr produced in 1951 was more abundant on plots from which rice tops had been removed, and this led to greater clover density and yields in the 1952 season. Where rice tops had been incorporated clover or grass yields did not differ between the gypsum treatments, but where rice tops had been removed clover yielded 20 per cent. higher on the gypsum-treated plots. The mean dry matter yield for all treatments equalled 56 cwt/acre of clover and 9 cwt/acre of ryegrass.

In 1953, when winter rains were light, yields did not noticeably differ between the treatments.

Clover seedlings, which established in April 1954, were concentrated along cracks in the soil. The soils were very wet during May, three irrigations having been followed by 0.90 in. of rain on April 29. Clover leaves were small and petioles were dull red, the condition being more pronounced where plants were located away from cracks or in minor depressions. Ryegrass plants were small and showed yellow and red tipping of the leaves. By May 18 the clover appeared to be growing more vigorously on the gypsum-treated plots and it yielded higher on these when

sampled on June 1, although the level of yields was low throughout the trial. Over the whole season clover yielded 13 per cent. higher on the gypsum-treated plots. Mean dry matter yield for all treatments equalled 51 cwt/acre of clover and 11 cwt/acre of ryegrass.

Yields did not differ between the 2 and 8 tons/acre rates of gypsum application in any season.

(*c*) *Discussion*

Addition of gypsum followed by flooding of Riverina clay for rice growing displaced sodium salts from the profile, but when this treatment was followed by intermittent irrigation of pastures, periods of net evaporation caused appreciable return of soluble sodium to the top 30 in. The extent of this return and its effect on exchangeable cations over a longer period will be reported in a later note.

Gardner (1945) noted that the clay floccules formed in alkali soils were voluminous, loosely packed, and easily redispersed. Such soils may be impermeable in the flocculated state. Sinicins (unpublished data, 1951) found that the settling volume of floccules of Riverina clay was reduced by the gypsum treatments. This change in settling volume of the floccular state is related to the reported reduction in the percentage dispersion after wetting and shaking and, in a qualitative way, to greater friability of the gypsum-treated soils.

Although no foliar symptoms of calcium deficiency were observed, it is possible that supply of calcium as a nutrient contributed to the increase in yield of subterranean clover. Calcium comprised 25-30 per cent. of the exchangeable cations in the top foot of Riverina clay. Stout (1949) reviewed data relating the degree of saturation with calcium to plant requirements, and concluded that deficiency could occur when the degree of saturation fell below 30 per cent. Sulphur reserves in the form of crystalline gypsum occurred below 30 in. depth in Riverina clay, and 30 lb/acre of sulphate was added in each foot of irrigation water. No foliar symptoms of sulphur deficiency were found. The greater incidence of yellow leaf tipping in rice grown on the gypsum-treated plots suggests that this widespread condition may be caused or aggravated by sulphide toxicity. Injury to lowland rice by the accumulation of reduced compounds in highly impermeable soils has been described by Sik (1950).

A high content of organic matter usually makes clay soil less sensitive to the effects of sodium, and it cannot be assumed that a yield response to gypsum will be obtained on old pasture land. Van Beekom and others (1953) note that stabilization of structure by organic matter makes it unnecessary to apply gypsum in order to restore grassland which has been inundated by sea-water. This effect of organic matter may account for the failure of subterranean clover to respond to gypsum in 1952 on those plots where rice tops had been incorporated. On the other hand, the addition of gypsum to Riverina clay has accelerated the rate of structural develop-

ment under pasture, as shown by the considerable decrease in apparent density found on gypsum-treated plots after 2 years' pasture growth.

VI. Conclusions

The soil changes brought about by flood fallow or by rice cropping without gypsum application did not result in any increase in the yield of irrigated annual pasture beyond the first growing season. The increase in the first season was mainly due to water remaining in the soil after inundation.

The application of gypsum followed by rice cropping removed most of the soluble salts from the top 30 in. of the soil. The treatments increased the water stability and the rate of structural development of the top few inches. This improvement in the physical condition of the soil did not lead to as great an increase in the yield of subterranean clover as anticipated. In two of the four seasons studied, no increase in yield was detected on the gypsum-treated plots, and in the other two seasons the yield increase was 10-20 per cent.

VII. Acknowledgments

The authors are greatly indebted to Mr. F. Arndt for assistance with the field and laboratory work carried out at Deniliquin, and to Mr. A. R. P. Clarke and Miss F. J. A. Doe for assistance with the laboratory work carried out at Adelaide. The authors also wish to thank Dr. N. I. Sinicins for helpful discussions and permission to quote his unpublished data.

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STUDIES IN THE ECOLOGY OF THE RIVERINE PLAIN

II. PLANT-SOIL RELATIONSHIPS IN THREE SEMI-ARID GRASSLANDS

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(*Manuscript received May* 31, 1955)

Summary

An experimental area on the semi-arid Riverine Plain originally supported *Eucalyptus* savannah woodland on sandy loams, *Acacia-Atriplex* dry scrub on clay loams, and *Atriplex* saltbush on light clays. Each of these communities has been replaced by a disclimax grassland. The species composition of the grassland is influenced by the soils. Differences in topography and texture are the main factors which affect the redistribution of rainfall. Soil permeability and subsoil structure are also important. The water regime of the soils over a 3-year period is measured in detail and the available moisture is estimated.

I. INTRODUCTION

The present paper describes studies of the vegetation in the Riverine Plain about Deniliquin, N.S.W., which represent a third stage in investigations which began with the general vegetation and pasture maps of Australia compiled by Prescott (1931), and by McTaggart (1936). The second stage was completed by later workers (Beadle 1948; Moore 1953*a*, 1953*b*) using the "primary survey" method (Tansley 1954). This method involves delineation of the major communities and the compilation of their species composition.

In Australia it has become a general practice at this point for the investigator to suggest the various ecological factors which may influence the distribution of the dominant species encountered in this primary survey. However, it is not often that the validity of these hypotheses is tested. This is the third or intensive stage of ecological investigation.

In paper I of the present series Williams (1955) showed that the species distribution within a disclimax grassland is very strongly influenced by the soil moisture regime and associated edaphic factors. In this paper, edaphic factors contributing to the development of three diverse grasslands in the climatic environment of the Riverine Plain are discussed. These factors may apply in principle over the more arid parts of the temperate short-grass zone defined by Christian and Donald (1949).

The three grassland communities described here are located at the Falkiner Memorial Field Station, C.S.I.R.O., Deniliquin. The experimental areas were ungrazed for 6 years prior to determination of the species composition in the July-October period of 1947.

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II. Environment

(*a*) *Climate*

The mean annual rainfall at Deniliquin is 15.72 in. (87 years), 56 per cent. falling in the cooler months from April to September. The remainder consists of erratic thunderstorms. The annual evaporation from a standard 36-in. tank at the station is 63.3 in. (4 years). The monthly rainfall and evaporation are set out in Table 1.

The effectiveness of summer rains is low because of high evaporation. Winter rainfall is more reliable than summer rainfall. Only 4 per cent. of years receive less than 5 in. in winter, but 28 per cent. receive less than this in summer.

Table 1

MONTHLY RAINFALL AND EVAPORATION AT DENILIQUIN (IN.)

Data	Jan.	Feb.	Mar.	Apr.	May	June	July
Rainfall	1.01	1.09	1.21	1.33	1.55	1.73	1.32
Evaporation	11.5	8.3	7.1	3.9	2.3	1.4	1.3
Data	Aug.	Sept.	Oct.	Nov.	Dec.		Total
Rainfall	1.45	1.45	1.50	1.06	1.02		15.72
Evaporation	2.1	3.4	4.9	7.0	10.1		63.3

Temperatures are high in summer, with an annual mean of 11 days exceeding 100°F and 63 days exceeding 90°. January is the hottest month, with a mean maximum temperature of 89.5° and a mean minimum of 61.0°. Four severe frosts (screen temperature below 32°) and 18 light frosts (screen temperature from 32° to 36°) are recorded annually. The frost-free period is 252 days. July is the coldest month, with a mean maximum temperature of 57.2° and a mean minimum of 39.0°.

(*b*) *Soils*

The regional topography of the Deniliquin area has been described by Butler (1950). This area is an alluvial plain consisting of clay, clay loam, and loam soil with a gradual slope away to the west and north. There are narrow bands of slightly higher country where the soils are sands and sandy loams. These levees traverse the plain in a digitate system. From the detailed survey by Butler and Johnston (1947) the soils under the three grassland communities were identified, and their important characteristics are given in Table 2.

The featureless plains have mean slopes of 0.05 per cent., and are impermeable when wet so that a high proportion of the rainfall runs into cracks, depressions, and swamps. The initial infiltration rate is high because the clay soils crack as they dry. In spite of this Tisdall (1948)

found that their overall infiltration rate is generally much lower than that of the coarse-textured soils.

Unlike the coarse-textured soils, the clay soils are a poor medium for plants, being difficult for either water or roots to penetrate.

TABLE 2

SOIL TYPE CHARACTERISTICS

Analytical data after Butler and Johnston (1947)

Topography	Surface Texture	Surface Depth (in.)	Reaction (pH)		Chloride (%)		Soil Type
			At 2 In.	At 12 In.	At 2 In.	At 12 In.	
Levees	Sandy loam	18-24	6.7	7.4	0.003	0.004	B
	Soils with a loose coarse-textured surface of high permeability. Cemented subsoils						
Higher portions of featureless plains	Clay loam	1-2	6.1	7.8	0.036	0.270	H
	Compact clay soils of low permeability. Small areas of gilgai microrelief						
Featureless plains	Light clay	0-1	7.1	9.0	0.002	0.032	R
	Clay soils with poorly structured subsoils of low permeability. Large areas of gilgai microrelief						

(*c*) *Vegetation*

Beadle (1948) and Moore (1953*a*) have completed ecological studies to the west and east of the Deniliquin area. Using Moore's classification, soil type B appears to have supported the *Eucalyptus woollsiana–Callitris glauca* association, and soil type H supported the *Acacia pendula–Atriplex nummularia* association. It appears likely that soil type R once supported a community dominated by *Atriplex nummularia* Lindl. This community would correspond to the *A. nummularia* type of Beadle (1948).

In a later paper Moore (1953*b*) describes the disclimax communities which exist on these soils at the present time. On coarse-textured soils similar to soil type B *Stipa falcata* Hughes becomes the dominant species, and *Danthonia* sp. is a minor constituent. On fine-textured soils *Danthonia* sp. may become a co-dominant (soil type H), or a dominant species (soil type R).

III. EXPERIMENTAL PROCEDURE

A qualitative survey was made on 1500 acres along traverses 5 chains apart, and a tentative map of the pasture community was prepared. Classification into communities was based on the density of perennial grasses.

Within each of the three pastures to be investigated four 2.5 acre replicates were selected at random. Each replicate was divided by tapes into 25 blocks (1 sq. chain in area). The botanical analysis of the perennial species was made by placing a 28-metre line along the diagonals from the north-west corner of each block. Modifications suggested by Roe (1947) were made to the Parker and Savage method, and 100 intercepts were completed in each pasture. The species composition is derived from the basal area data. The specific frequency is the number of times one or more plants of a particular species occur in the 100 transects completed in each pasture. At the same time the abundance of annual species in each replicate was assessed using the five-point scale of Braun-Blanquet (1932).

Investigations by Williams (1955) had shown the influence of the soil moisture regime on the flora of the gilgai microrelief and this approach was again utilized.

The soil moisture percentage retained against a pressure of 15 atm (pF 4.2) was obtained for samples from the 0-3 in., 3-9 in., and 9-18 in. depth of each soil using the pressure membrane apparatus devised by Richards and Weaver (1943).*

Soil moisture percentages were determined from samples taken fortnightly during 1951, 1952, and 1953 at four sites in each pasture. Four cores were taken with a sampling tube at the 0-3 in., 3-9 in., and 9-18 in. depth. The soil was bulked and subsampled for each depth at each site.

The chloride concentration of individual soil cores taken during June 1952 was obtained in duplicate from electrometric titrations using silver nitrate (Piper 1942). The osmotic term of soil moisture stress was calculated on the assumption that all chlorides were sodium chloride and were in solution at the 15 atm percentage.

Available moisture for plant growth was calculated as the difference between the 15 atm percentage and the maximum value of soil moisture during 1951, 1952, and 1953. Allowance was made for the osmotic term of moisture stress. Field capacity could not be estimated because of the poor internal drainage in soil types H and R, and the cemented subsoil in soil type B.

Bulk density was determined over a range of soil moisture values for each soil using the apparatus of Coile (1936). This procedure overcame errors due to loss of cohesion at high moisture levels in soil type B. In the clay soils the moisture volume at specified soil moisture percentages was calculated from correlations established between soil moisture and bulk density.

* These determinations were made by Dr. J. P. Quirk, Division of Soils, C.S.I.R.O., Adelaide.

TABLE 3

SPECIES COMPOSITION OF PASTURE COMMUNITIES

Perennial Species	*Stipa falcata* (soil type B)			*S. falcata–Danthonia caespitosa* (soil type H)			*D. caespitosa* (soil type R)		
	Specific Frequency	Basal Area (%)	Species Composition	Specific Frequency	Basal Area (%)	Species Composition	Specific Frequency	Basal Area (%)	Species Composition
GRASSES									
Aristida behriana F. Muell.	13	0.023	1.5						
Enneapogon nigricans (R.Br.) Beauv.	5	0.006	0.4						
Stipa falcata Hughes	100	1.287	82.3	98	0.554	36.4	20	0.032	3.4
Danthonia caespitosa Gaud.	32	0.035	2.2	97	0.482	31.7	99	0.648	69.6
Chloris truncata R.Br.	15	0.008	0.5	83	0.155	10.2	28	0.024	2.6
Sporobolus caroli Mez				30	0.021	1.4	18	0.013	1.4
Chloris acicularis Lindl.				9	0.012	0.8	1	0.002	0.2
Unidentified (2)	24	0.061	4.1	3	0.002	0.1			
Total grasses:		1.420	91.0		1.226	80.6		0.719	77.2
CHENOPODIACEAE									
Salsola kali L.	32	0.011	0.7	4	0.002	0.2			
Kochia tomentosa (Moq.) F. Muell.	11	0.005	0.3	4	0.001	T			
K. crassiloba R. H. Anderson	2	0.001	0.1	1	T	T			
K. ciliata F. Muell.	1	T	T	83	0.071	4.7	82	0.087	9.3
K. tomentosa var. *tenuifolia* F. Muell.	1	T	T	1	T	T	19	0.005	0.5
Atriplex semibaccata R.Br.	4	0.024	1.5	5	0.035	2.3	11	0.028	3.0
Bassia quinquecuspis F. Muell.	2	T	T	7	0.005	0.3	63	0.023	2.5
Chenopodium multifidum L.	1	0.007	0.5	18	0.012	0.8	1	T	T
Kochia excavata J. M. Black				87	0.074	4.9	1	T	T
K. aphylla R.Br.				3	0.001	T	4	0.005	0.5
Total Chenopodiaceae:		0.047	3.1		0.201	13.2		0.148	15.8

*T, trace.

TABLE 3 (*Continued*)

Perennial Species	*Stipa falcata* (soil type B)			*S. falcata–Danthonia caespitosa* (soil type H)			*D. caespitosa* (soil type R)		
	Specific Frequency	Basal Area (%)	Species Composition	Specific Frequency	Basal Area (%)	Species Composition	Specific Frequency	Basal Area (%)	Species Composition
OTHER HERBS									
Lomandra effusa (Lindl.) Ewart	19	0.062	4.0						
Vittadinia triloba (Gaud.) DC.	10	0.004	0.2						
Sida spp. (2)	62	0.019	1.2	94	0.025	1.6			
Goodenia subintegra F. Muell.	6	T	T	63	0.008	0.5			
Ptilotus spp. (2)	8	0.002	0.1	55	0.038	2.5	1	T	T
Wahlenbergia gracilis (Forst. f.) DC.	23	0.004	0.2	1	T	T	38	0.006	0.6
Teucrium racemosum R.Br.	4	0.001	0.1	22	0.003	0.2	3	T	T
Swainsona behriana F. Muell.	1	T	0.1	25	0.010	0.6	1	T	T
Helichrysum apiculatum (Labill.) DC.				10	0.009	0.6			
Solanum esuriale F. Muell.				2	T	T			
Calotis scabiosifolia Sond. & F. Muell.				5	0.001	0.1	61	0.036	3.8
Bulbine bulbosa (R.Br.) Haw.				5	T	T	1	T	T
Swainsona procumbens F. Muell.				4	0.001	0.1	1	T	T
Plantago varia R.Br.							47	0.009	0.9
Leptorhynchus panaetioides Benth.							7	0.005	0.6
Muehlenbeckia cunninghamii F. Muell.							1	0.001	0.1
Unidentified (1)	4	T	T						
Total other herbs:		0.093	5.9		0.095	6.2		0.066	7.0
TOTAL PERENNIAL SPECIES		1.560	100.0		1.522	100.0		0.933	100.0
Basal area of dominant grass (%)		1.287			1.04			0.65	
Contributions by dominant grass (%) of total basal area		82.3			68.1			69.6	

*T, trace.

IV. Results

(a) *Vegetation*

Perennial grasses are the most important group of plants and occupy the greatest basal areas. Statistical analyses of line interception data were made and confirmed the impression that differences between the dominant grasses in the three communities were significant. The species composition calculated from basal area measurements, and the specific frequency for all perennial plants, are set out in Table 3. This table also shows the basal area of the two dominant grasses and the contribution they make to the total basal area in each community.

The total basal area of 0.93-1.56 per cent. occupied by perennial plants in these grassland communities is very low compared with the 15 per cent. recorded in the New England district by Roe (1947) on *Danthonia*-dominant pasture.

The abundance of annual species in the three communities is set out in Table 4.

(i) Stipa falcata *Community*.—This community occurs on light-textured soils of the levees, and *S. falcata* is often the only perennial grass. *Aristida behriana* and *Enneapogon nigricans* were limited to soils with a deep A horizon. *Lomandra effusa* and *Stipa aristiglumis* F. Muell. imparted a characteristic facies to the community at two sites. *S. aristiglumis* was not recorded in the intercepts, but the few plants in the community were quite obvious because they were 4 to 6 ft high.

Of the 20 perennial plants recorded, only two occurred in more than 50 per cent. of intercepts, whereas 11 of the 19 annual species recorded in the abundance list were well distributed over the sample sites. This indicates the strongly ephemeral character of the community.

The root systems of most plants are limited to the 0-18 in. depth, but *Sida corrugata* Lindl., *Wahlenbergia gracilis*, and *Vittadinia triloba* penetrate the hardpan and grow in the underlying loam and clay loam subsoils.

(ii) Stipa falcata–Danthonia caespitosa *Community*.—This grassland is located on higher levels of the plain adjacent to the levees. *Stipa falcata* is the main grass on the plain and associated species include *Kochia aphylla, K. excavata, K. ciliata, Danthonia caespitosa, Ptilotus spathulatum* R.Br., *P. obovatum* Lindl., *Sida corrugata*, and *S. trichopoda* F. Muell. Scattered over the plain are two types of small depressions from 2 to 4 ft in diameter. In depressions with a massive surface soil *Danthonia caespitosa* is dominant and *Stipa falcata* is subdominant. When the surface of the soil is loose two short-lived perennial grasses *Chloris truncata* and *Sporobolus caroli* replace them. *Medicago denticulata* and *M. praecox* are the dominant herbs. Species not recorded in the intercepts but present in the sample area included *Muehlenbeckia coccoloboides* J. M. Black, *Anguillaria dioica*

R.Br., *Arthropodium minus* R.Br., *Leptorhynchus panaetioides* Benth., and *Kochia aphylla.*

TABLE 4

ABUNDANCE OF ANNUAL SPECIES IN PASTURE COMMUNITIES

After Braun-Blanquet (1932). 1, Very rare; 2, rare; 3, infrequent; 4, abundant; 5, very abundant

Species	Pasture Community		
	Stipa falcata (soil type B)	*S. falcata–Danthonia caespitosa* (soil type H)	*D. caespitosa* (soil type R)
Helipterum australe (A. Gray) Druce	4		
Trifolium arvense L.	4		
T. glomeratum L.	3		
Sisymbrium officianale L.	3		
Helipterum variabile (Sond.) Ostenf.	4	4	
Crassula colorata Ostenf.	5	2	2
Goodenia pusilliflora F. Muell.	5	4	4
Asperula conferta Hook. f.	4	3	3
Calotis hispidula F. Muell.	4	2	2
Helipterum pygmaeum (DC.) Benth.	4	2	2
Vulpia myuros (L.) Gmel.	4	3	2
Matricaria discoides DC.	4	4	3
Hordeum leporinum Link.	3	2	2
Helipterum corymbiflorum Schlech.	3	4	5
Euphorbia drummondii Boise.	2	3	3
Medicago denticulata Willd.*	2	3	4
Erodium cygnorum Nees	5		2
Helipterum albicans (A. Cunn.) DC.	3		2
Erodium cicutarium (L.) L'Hérit.	3		2
Eriochlamys behrii Sond.		5	4
Daucus glochidiatus (Labill.) Fisch., Mey. & Ave-Lall.		3	4
Isoetopsis graminifolia Turcz.		3	4
Medicago tribuloides Gaertn.		2	2
Calocephalus sonderi F. Muell.			4
Sonchus oleraceus L.			3
Bromus rubens L.			3
Chenopodium atriplicinum F. Muell.			3
Number of species in each pasture	19	16	22
Total number		27	

* Also includes *Medicago praecox* DC.

Of the 16 annual species listed only five were well distributed. Eight of the 27 perennial species were present on more than 50 per cent. of the intercepts.

The root systems of most plants are restricted to the shallow surface soil and to cleavage planes in the poorly structured subsoil. Roots seldom penetrate deeper than 18 in.

(iii) Danthonia caespitosa *Community.*—This grassland occurs on the lower levels of the plain where the gilgai microrelief is widespread. Williams (1955) in a study of this vegetation has shown that each soil component can give rise to a characteristic plant community. The relative contribution to ground surface within the sample areas by the shelf, depression, and puff therefore determines the species composition of the community.

Danthonia caespitosa is the dominant perennial grass and is situated in a mesic environment. The Chenopodiaceae, represented by the genera *Atriplex, Bassia, Chenopodium,* and *Kochia,* are located on the more xeric areas. Water lies in the depressions for short periods and representatives of the genera *Juncus, Eleocharis, Carex, Cyperus,* and *Amphibromus* have been identified after heavy winter rainfall. This grassland consists of a mosaic of three distinct communities each of which has a different water requirement.

Seven of the 22 annual plants were widely distributed, but only four of the 22 perennial species were recorded in more than 50 per cent. of the intercepts.

Root systems in the shelf and depression components are limited to the shallow surface soil and to cleavage faces in the poorly structured subsoils. Root systems in the well-structured puff extend to 18 or 24 in.

As the soil texture changes from sandy loam under the *Stipa falcata* community to clay under the *Danthonia caespitosa* grassland, there is a decrease in both total basal area, and basal area of the dominant species. *Stipa falcata* is replaced by *Danthonia caespitosa* and there is a progressive increase in the contribution of the Chenopodiaceae to the species composition.

(*b*) *Soils*

Underlying the *Stipa falcata* grassland at 18 in. there is an impervious hardpan, and under the communities which have developed on clay soils moisture changes are limited in general to the top 18 in. The relevant moisture data are summarized in Table 5.

More water is available for plant growth under the *Stipa falcata* grassland than is the case for other communities. The depression soils require the greatest volume of water to raise soil moisture from the midsummer value to the maximum. The difference between potential and actual values measures the permeability of the soil.

In the absence of transpiration determinations it is assumed that the moisture uptake by roots quickly dries the entire root zone in sandy loams supporting the *Stipa falcata* grassland. This community offers the greatest

surface area from which transpiration may occur. The clay soils underlying the other communities swell and shrink with wetting and drying, and the soil is not as thoroughly explored by roots as the sandy loams. Most root systems are limited to cleavage planes. Isolated pockets of soil moisture may occur at depth for some months after rainfall because of run-off.

TABLE 5

AVAILABLE SOIL MOISTURE IN THE 0-18 IN. DEPTH UNDER THREE GRASSLAND COMMUNITIES (IN.)

Community	Soil Type	Potential*	Actual†	Difference	Permeability
Stipa falcata	B	2.13	2.13 (3.03)‡	0	Good
S. falcata–Danthonia caespitosa	H	1.60	1.05 (2.74)	−0.55	Poor
D. caespitosa:	R				
Shelf		1.21	0.57 (2.68)	−0.64	Very poor
Depression		2.32	1.71 (3.38)	−0.61	Very poor
Puff		1.50	1.15 (3.15)	−0.35	Good

*Potential value obtained by summation of maxima during 1951, 1952, and 1953 for 0-3, 3-9, and 9-18 in. depths.

†Actual maximum value obtained from 0-18 in. depth at one sampling date.

‡Values in brackets are inches of moisture required to raise soil from the lowest moisture content to the actual recorded maximum during 1951, 1952, and 1953.

The chloride content under the grassland communities was determined from soil samples taken during the growing season (June). The results are set out in Table 6.

TABLE 6

CHLORIDE CONTENT OF SOILS UNDER THREE GRASSLAND COMMUNITIES

Values given as per cent. dry weight of soil

Depth (in.)	*Stipa falcata*	*S. falcata–Danthonia caespitosa*	*D. caespitosa*		
			Shelf	Depression	Puff
0-3	0.004	0.009	0.010	0.008	0.006
3-9	0.005	0.024	0.057	0.007	0.008
9-18	0.005	0.175	0.183	0.040	0.020

The chloride concentration is low in the 0-9 in. depth under all communities, but is significantly greater in the 9-18 in. depth of the *Stipa falcata–Danthonia caespitosa* grassland, and the shelf component of the *Danthonia caespitosa* grassland, than under the other communities. Water moves very slowly through the soil above these horizons, and root growth could be restricted either by chloride concentration or by lack of moisture. In the vicinity of soil cracks at this depth the effect of the chloride on plants is appreciably reduced by the higher soil moisture.

The aeration of soil under the grassland communities was measured by air-space determinations in wet soil. The results are set out in Table 7.

In the depression, air space appears inadequate for the growth of the more usual semi-arid plants, and species which tolerate these poor conditions occur frequently after heavy and prolonged rainfall. They include *Juncus* spp., *Eleocharis* spp., and *Marsilea drummondii* R.Br.

TABLE 7

AIR SPACE IN 0-3 IN. DEPTH UNDER THREE GRASSLAND COMMUNITIES AT THE MAXIMUM MOISTURE CONTENT, 1951-1953

Values given as per cent. volume

Community	Soil Type	Air Space	Permeability
Stipa falcata	B	23.5	Good
S. falcata–Danthonia caespitosa	H	14.9	Poor*
D. caespitosa:	R		
Shelf	0-½ in.	13.6	
	½-3 in.	16.5	Very poor*
Depression		5.5	Very poor
Puff		25.3	Good

*Run-off from these into depressions.

V. DISCUSSION

In the *Stipa falcata* community, water is readily available after light rainfall in the surface soil because of the small amount required to raise the soil to the 15 atm percentage. Recharging of the water-holding capacity is rapid, and run-off is small, because up to 3 in. can be stored in this very permeable soil. Root systems develop strongly and plants extract moisture rapidly, presumably because of their large transpiring surface. Therefore this soil, which can store the greatest amount of available moisture, can have the store exhausted in a short time. As a result of this the vegetation on a sandy loam alternates between the community dominated by mesomorphic herbs, e.g. *Erodium cygnorum*, and a xeromorphic grassland dominated by *Stipa falcata*. In this investigation the botanical determinations were made during the latter phase.

In the *Stipa falcata–Danthonia caespitosa* grassland run-off into cracks occurs at an early stage during intensive rainfall. The surface soils seldom hold much available water because of their low permeability. Drainage into soil fissures forms occasional large bodies of saturated subsoil. Xeromorphic plants, including *Kochia aphylla*, *K. ciliata*, and *K. excavata*, tap these saturated pockets, producing green material in summer when few species are able to grow actively without frequent rainfall. However, the volume of this production is small. *Stipa falcata* develops a much restricted but intensive root system in the lighter-textured surface soil. Plants are less vigorous than those on sandy loam soils and the leaf area

from which transpiration occurs is much less. The ephemeral flora, including *Helipterum* spp., *Goodenia* spp., and *Daucus glochidiatus*, develops on this site during the more reliable winter rainfall period. *Danthonia caespitosa* is limited to fissured areas and small depressions which receive extra moisture.

In the *Danthonia caespitosa* grassland the perennial flora on areas of shelf soil is sparse and xeromorphic. Ephemeral herbs including *Helipterum* spp. are common. The depressions are populated by mesomorphic perennials and occasional hydrophytes including *Marsilea drummondii* and *Juncus* spp. Areas of puff soil are well drained because of their loose surface, and run-off does not occur. This soil structure facilitates good moisture penetration and root systems are well distributed. After good rainfall in winter large plants of *Medicago* spp., *Sonchus oleraceus*, *Avena fatua* L., and *Phalaris minor* Retz. rapidly reduce the soil moisture supply. This is followed by limited growth of the xeromorphic constituents, and so parallels changes that occur on the permeable soils underlying the *Stipa falcata* community. The high chloride percentage in the 9-18 in. depth of the shelf component is not important in this arid soil. The effects of inadequate air space are frequently observed in depressions and occasionally in lower parts of the shelf.

The species composition of the grassland communities in the semi-arid environment provided by the Riverine Plain appears to be greatly influenced by the water-soil relationship. Redistribution of rainfall is affected by textural and structural differences between soils. A xeromorphic flora develops where run-off commences and a hydrophytic flora where it ends. It is probable that the maximum water-holding capacity of the soils is not as important as their rate of recharge. In soils of high permeability this may be rapid, but in soils of low permeability the recharge of subsoil moisture may occur only through deep cracks. The association in some subsoils of high chloride percentages with low available soil moisture makes it difficult to assess the relative importance of these factors in the growth of root systems. However, the flora which develops on these areas is always xeromorphic, and many species are tolerant of high chloride levels. Because of the low transpiration per unit soil volume this type of community remains vegetative for longer during rainless periods than communities on soils which appear to have a better soil moisture regime.

VI. Acknowledgments

Grateful acknowledgments are made to colleagues at the Regional Pastoral Laboratory and the Falkiner Memorial Field Station, Deniliquin, for assistance with the experimental work.

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SELECTION FOR ECONOMIC CHARACTERS IN AUSTRALIAN MERINO SHEEP

VII. INTERACTIONS BETWEEN GENOTYPE AND PLANE OF NUTRITION

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(*Manuscript received October* 10, 1955)

Summary

A number of groups of half-sibs were divided into two lots, one being exposed to a high plane of nutrition, the other to a low plane, from 3 to 17 months of age.

Heritability, as indicated by the within sire correlation, did not vary with plane of nutrition.

Genotype-treatment interactions were not present for any fleece characters or for 6-month body weight. Such interactions were large and highly significant for weight at 12 or 17 months.

These findings indicate that the opinions of Hammond (1947) are not generally valid.

I. Introduction

Falconer (1952) and Falconer and Latyszewski (1952) have discussed some aspects of the general problem of environment and selection. In particular they have criticized views, expressed by Hammond (1947), that environmental conditions, if unfavourable, will prove to be a factor limiting the response to selection. While there can be little disagreement with some of Hammond's conclusions, the selection experiments of Falconer and Latyszewski (1952) have certainly cast doubt on the general validity of his claims. These authors selected mice for 6-week weight under high and low planes of nutrition. Heritability, as estimated by selection response, was higher (not significantly) on the low plane of nutrition. The genetic correlation between growth on the low plane and that on the high plane was about 0.6. The experiment thus gave no support for some of Hammond's views, and indicated little justification for selection in any environment other than the one in which progeny are expected to perform.

Australian Merino sheep are exposed to wide geographical and year-to-year variations in environment. Certain strains appear best adapted to some areas, but strains are sympatric over extensive regions. Strains such as the Peppin Merino are widely distributed through most important wool-producing areas, and are thus exposed to almost the whole range of environments. In addition, the spectacular fluctuations in food supply

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characteristic of many environments render almost meaningless terms such as "average nutritional regime". Because of these circumstances investigations of genotype-environment interactions in Merino sheep are of obvious importance.

In a breed such as the Merino we may investigate genotype-environment interactions with genotypes at at least three levels. Genotypes may vary among strains, among flocks within strains, and within flocks. In this paper we shall consider only variation within a flock. From the viewpoint of selection within a closed flock this is the only level which is relevant.

Environmental levels of variation could take into account a wide array of combinations of at least temperatures, nutrition, photoperiods, and systems of management. We shall consider, as far as possible, only nutrition. This is probably the most important variable from district to district, and also from year to year within the one district. Clearly, if nutritional levels fluctuate violently, as they do from year to year, and if there are important nutrition-genotype interactions, the effectiveness of selection may be severely prejudiced.

We shall endeavour to answer two important questions. First, is the heritability dependent on the plane of nutrition? Second, is selection in one regime of limited value for another regime? In other words, are genotype-environment interactions important?

II. Methods and Materials

(*a*) *Sheep of Experiment*

The sheep were portion of the experimental flock at Trangie Agricultural Experiment Station (see Morley 1951, 1955). The genetic variability of this material was made as large as possible by using small flocks in which selection had been directed for and against clean fleece weight and crimps per inch. An additional group consisted of offspring of progeny-tested sires and selected ewes. All sheep in the experiment were born in February-March 1953. Each sire group was divided into two portions, one being kept on a high plane and the other on a low plane. Numbers in each portion were as far as possible the same. For the purposes of this analysis numbers were made equal by discarding at random.

(*b*) *Planes of Nutrition*

Sheep on the high plane were given the best available grazing. Where this seemed limiting, supplementary feed (cereal or medic hay, oaten grain, meat meal, and ground limestone) was offered *ad lib*. As far as possible a frequent check on the condition of sheep was maintained by weighing a marked sample at 2-weekly intervals. Lambs destined for the low plane group were weaned on June 4, 1953, onto good pasture. They were transferred to poor pasture on June 18. Lambs on the high plane

were weaned on June 30. The low plane was achieved by keeping sheep on pastures which had been or were heavily rabbit-infested and on which little feed was offering. During the spring flush of growth systematic starvation was attempted by confinement to yards for 2-day periods. For humanitarian reasons this treatment was not applied frequently and sheep gained weight more quickly than desired. However, as shown in Figure 1, clear distinction was achieved between treatments.

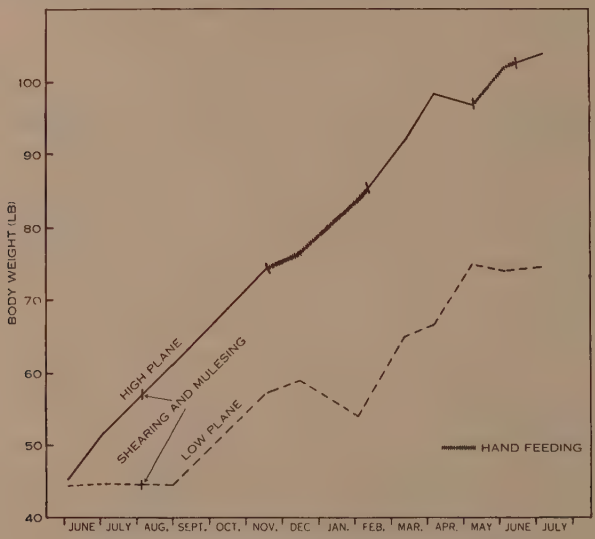

Fig. 1.—Body weights of treatment groups.

(*c*) *General Management*

Lambs were shorn in the first week of August 1953, after which they were treated by the radical Mules operation. Moderately good conditions were provided for the low plane group for 3 weeks after these operations, which, combined with the spring growth, resulted in a substantial weight increment. Treatments ceased on July 8, 1954, and the two groups were then run together on a fairly low plane of nutrition. Because of wet weather, shearing was delayed until the second week in August. Apart from regulation of the plane of nutrition, management followed the usual routine.

(*d*) *Analysis*

All data were transformed to logarithms in order to equalize variances within treatments. The intraclass correlation among half-sibs was estimated by the usual methods within each treatment. The combined analysis of the two treatments and estimation of components of variance followed the usual lines.

III. Results

The antilogarithms of the mean logarithms for each characteristic in each treatment are presented in Table 1.

Apart from yield and crimps per inch the differences between treatments are impressive and indicate success in inducing environmental differences.

Results from within treatment and combined analyses of variance are presented in Table 2. Within treatments there were 23 degrees of freedom among sires, 53 for residual. In the combined analysis there was 1 degree of freedom for treatments, 23 for both sire and interaction, and 106 for residual. The estimated components of variance have been converted to standard measure.

Using the method of establishing fiducial intervals for variance components (Bross 1950), there were no indications that intraclass correlations differed between treatments for any character.

Estimates of the interaction components were zero or slightly (certainly not significantly) negative for all characters except body weights at 12 and 17 months of age. In these the interaction components were large and highly significant. Interactions were most unlikely to occur and were not found where main effects, either genetic (staple length) or treatment (yield, or crimps per inch), were small.

IV. Discussion

The results of Table 2 certainly give no indication that the ratio of genetic to total variance has been affected by plane of nutrition. The data on ratios of standard deviations in Table 1 do not suggest that the percentage response would vary with plane of nutrition. The results therefore appear to contradict Hammond, who stated (1947, p. 209) that ". . . it is only possible to direct evolution by the selection of genes for these characters under circumstances where the environmental conditions are optimal for the development of the character in question".

Nevertheless it must be admitted that the apparent contradiction may not be an entirely valid criticism of Hammond's statement. Genetic variation on the low plane may be the expression of a character such as foraging ability or efficiency of utilization whereas on the high plane the character concerned may be appetite, ultimate size, or even placid temperament. This question is discussed generally by Falconer (1952). If the genotypes for high expression of a character in one environment were different from those for a high expression in another environment, this would be indicated by a genotype-environment interaction. Such interactions are present and highly significant for body weights at 12 and 17 months but not for fleece weight or 6-month body weight. The results therefore indicate that fleece production on one plane of nutrition provides a good indication of that on another plane. But this is not true for body

TABLE 1

ANTILOGARITHMS OF MEAN LOGARITHMS OF TREATMENT GROUPS AND RATIO OF RESIDUAL STANDARD DEVIATION (LOW : HIGH)

Nutritional Level	Greasy Fleece Weight (lb)	Yield (%)	Clean Fleece Weight (lb)	Staple Length (cm)	Crimps per Inch	Body Weight (lb) at		
						Aug. 1953	Feb. 1954	July 1954
High plane	13.2	61.2	8.0	10.0	10.8	60.7	83.5	103.4
Low plane	9.4	60.2	5.6	8.9	10.4	44.2	53.3	72.9
Difference	3.8*	1.0	2.4*	1.1*	0.4	16.5*	30.2*	30.5*
Ratio $s_l : s_h$	0.83	0.81	1.15	0.81	1.20	1.28	1.06	1.34

* Significant at $P < 0.001$.

TABLE 2

WITHIN PLANE, INTRACLASS CORRELATION AMONG HALF-SIBS AND ESTIMATES OF COMPONENTS OF VARIANCE IN COMBINED ANALYSIS

Characteristics	Intraclass Correlation		Components of Variance			
	High	Low	Plane	Sire	Interaction	Residual
Greasy fleece weight	0.31**	0.31**	4.70**	0.46**	0	1.0
Yield	0.24**	0.44**	0	0.61**	0	1.0
Clean fleece weight	0.52**	0.39**	3.81**	0.85**	0	1.0
Staple length	0	0	0.68**	0.02	0	1.0
Crimps per inch	0.22**	0.25**	0.09	0.39**	0	1.0
Body weight:						
6 Months	0.11	0.10	2.87**	0.13*	0	1.0
12 Months	0.36**	0.29**	8.38**	0.11	0.56**	1.0
17 Months	0.26**	0.40**	6.03**	0.17	0.42**	1.0

* $P < 0.05$. ** $P < 0.01$.

weight at later stages of growth. Therefore the generalizations advanced by Hammond cannot be valid, for if correct in one case they must be incorrect in another. Further, a generalization from observations on one character may not be valid for another, even within the same strain.

These findings have clear implications in commercial breeding practice. We have shown that genotype-nutrition interactions are present in at least one important trait. The fact that they were not found for fleece weight does not indicate that similar interactions, for example, genotype-temperature, may not exist for fleece weight. The only safe course must be to select in a "commercial" environment. The present results suggest that, with respect to plane of nutrition, the present organization of Merino sheep breeding, with stud sheep generally on relatively high planes of nutrition, may be quite satisfactory for fleece characteristics but not so for body weight. The genetic correlation between the characteristics determining body weight on high and low planes, which may be written $S/(S + I)$, if S is the sire and I the interaction component, is approximately 0.16 at 12 months and 0.29 at 17 months. That is, selection for high body weight under one plane of nutrition may be only 15 to 30 per cent. effective under another. However, the position may not be nearly as serious as suggested by these results, since the differences between planes of nutrition in this experiment were more extreme than those commonly encountered in practice.

The absence of a genotype-treatment interaction for fleece weight, and its presence for body weight, has an important bearing on some current discussions on the biology of fleece growth. Fleece weight per sheep has been considered by Galpin (1947) to be largely determined by total surface area, since *inter alia* she interpreted her results as indicating that production per unit area was, under good conditions, constant over all sheep. The findings of Marston (1948) certainly do not support her conclusion, nor do the results of Morley, Lockart, and Davis (1955), although these could not be wholly conclusive since conditions were not at all times optimal. The results of this investigation, together with the zero genetic correlation between body weight and fleece weight (Morley 1955), indicate that genetically fleece weight and surface area (which is a function of body weight) are independent, the correlation between them being environmental in origin, both characters reacting in the same direction to nutritional variations. Since genotypes vary in their body-weight response, but not in their fleece-weight response, it seems most unlikely that wool production per unit area would be constant. The method of correcting fleece weight for body weight (Morley 1955), or estimating fleece weight from a function of body weight and production per unit area (Morley, Lockart, and Davis 1955), may select those individuals with a poor body-weight response in the first case or with a large response in the second. As a further study of these questions is being undertaken detailed discussion will be postponed.

Finally, attention is drawn to the value of the experimental method used in this investigation. Estimation of genotype-environment interactions, as undertaken by Falconer and Latyszewski (1952), is impracticable in livestock because of the number of generations required and the necessity for avoiding temporal variations in environment. The value of lines selected for and against specific characters in experiments such as these constitutes a powerful argument for forming them. The variance among sires was for most characters three or four times larger than would be expected in a random-bred flock. That is, the same amount of information was obtained as would have been from three or four times the number of random-bred experimental animals.

V. Acknowledgments

The data for this analysis are portion of the results of an experiment which was being supervised by the late Mr. L. Tomlinson until his recent death. I wish to record my thanks to him, and also to Mr. R. Dun and Prof. G. L. McClymont for assistance and many stimulating discussions.

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THE REACTION OF PRIMARY AND SECONDARY WOOL FIBRES TO CHANGES IN NUTRITION

By The Late L. W. Lockart*

(*Manuscript received November* 23, 1955)

Summary

The responses of primary and secondary wool fibres to changes of nutrition are in proportion to their cross-sectional areas. No indication was found that primary fibres compete more effectively with secondary fibres at a low level of wool production than at a high one.

I. Introduction

Lang (1945) suggested that the reactions of primary and secondary follicles to changes in nutrition may differ. This suggestion was supported by the observation that the mean fibre diameter was actually greater in some "tender" regions than either above or below these regions. If the thickest fibres, presumed to be the primaries, were relatively unaffected by adverse nutrition but the finer secondary follicles ceased production, such a result would be expected. But such reactions would be unexpected if the concepts of follicle efficiency (Fraser 1952) and follicle competition (Fraser and Short 1952) were applicable, and follicles retained their relative efficiencies in the mature animal irrespective of the level of nutrition.

In order to determine whether primary follicles differed from secondary follicles in their reactions to nutrition a series of measurements of diameters of primary and secondary fibres were made on sheep at different levels of nutrition.

II. Methods and Material

(*a*) *Experiment* 1

Two skin sections were taken from each of 32 rams, the first in September 1952 and the second in May 1953. In September excellent nutritional conditions prevailed but in May conditions were generally unfavourable. The major and minor diameters of 50 primary and 50 secondary fibres were measured on each section in each period.

(*b*) *Experiment* 2

Three adult ewes on a high plane of nutrition were placed on a low plane of nutrition. Skin sections were taken from the midside each 2 weeks,

*New South Wales Department of Agriculture, Agricultural Experiment Station, Trangie, N.S.W. Mr. Lockart was killed in an aircraft accident in May 1955. This communication was compiled by F. Morley from unpublished material. The assistance of Dr. B. F. Short and Dr. A. S. Fraser is acknowledged with thanks.

and from the rump at sampling times 2, 4, and 8. Body weights were measured weekly.

The characteristic analysed was the cross-sectional area calculated from the major and minor diameters.

III. Results

(*a*) *Experiment* 1

Analyses of variance of the product of major and minor diameters, and of the logarithm of this product, are given in Table 1.

Table 1

ANALYSIS OF VARIANCE OF MAJOR × MINOR DIAMETERS OF PRIMARY AND SECONDARY FIBRES OF 32 RAMS MEASURED ON TWO OCCASIONS

Source of Variation	D.F.	Arithmetic		Logarithmic	
		M.S. × 10^{-4}	*F*	M.S.	*F*
Among sheep	31	880	179	25902	195
Among fibre types	1	2276	464	45444	342
Periods	1	11915	2427	448398	3371
Sheep × types	31	1888	38	4486	34
Sheep × period	31	96	19.5	3730	28
Period × type	1	23	4.7	311	2.3
Residual	6303	5	—	133	—

If fibre types vary appreciably in response to nutrition one would expect the type × period interaction mean square to be significant. In fact this interaction is significant in the arithmetic analysis but is not so

Table 2

BODY WEIGHTS AT SAMPLING TIMES

Sampling No.	Body Weight (lb)		
	Sheep 1	Sheep 2	Sheep 3
1	112	90	105
2	106	91	101
3	102	86	96
4	98	82	90
5	96	80	89
6	95	81	85
7	92	78	82
8	89	73	80

in the logarithmic analysis. We may therefore conclude that there is no important difference in the *relative* response of the two types of fibre. This suggestion is supported by the fact that the fibre area in September relative to that in May was 148 per cent. for primaries and 151 per cent. for secondaries. If follicle output were considered, by including length, the period × type interaction might well decrease even further.

(*b*) *Experiment* 2

Body weights of the three sheep at the eight sampling dates are given in Table 2.

Table 3 gives the mean cross-sectional areas, in square microns, of the primary and secondary follicles for each period for the midside position.

TABLE 3
MEAN FIBRE AREAS
P, primary fibres; *S*, secondary fibres

Sampling No.	Mean Fibre Areas (μ^2) for					
	Sheep 1		Sheep 2		Sheep 3	
	P	*S*	*P*	*S*	*P*	*S*
1	611	518	470	486	910	412
2	537	409	363	331	619	331
3	467	401	360	297	672	278
4	354	305	376	341	565	287
5	370	256	334	280	367	305
6	545	267	306	248	633	338
7	407	345	315	220	372	160
8	311	255	354	229	367	192
Mean	450	345	360	304	563	288

Both primary and secondary fibre diameters decrease. If primary and secondary fibre diameters alter in proportion to cross-sectional areas, then the ratio of mean primary area to mean secondary area should remain reasonably constant. These ratios are given in Table 4.

TABLE 4
RATIOS OF MEAN AREA OF PRIMARY FIBRES TO MEAN AREA OF SECONDARY FIBRES FOR THE EIGHT SAMPLING PERIODS

Sampling No.	Ratios for			Mean Ratios
	Sheep 1	Sheep 2	Sheep 3	
1	1.18	0.97	2.21	1.45
2	1.31	1.10	1.87	1.43
3	1.16	1.21	2.42	1.60
4	1.16	1.10	1.97	1.41
5	1.45	1.19	1.20	1.28
6	2.04	1.23	1.87	1.71
7	1.18	1.43	2.33	1.65
8	1.22	1.55	1.91	1.56

There is no strong or consistent relationship between the ratio of primary area to secondary area and the mean diameter. A negative regression would be expected if primary fibres preferentially utilized fibre substrate.

The rump samples were taken to see whether differences between regions on the sheep varied proportionally, as would be expected. The mean fibre cross-sectional areas of the rump samples are given in Table 5.

TABLE 5

MEAN FIBRE CROSS-SECTIONAL AREAS OF PRIMARY AND SECONDARY FIBRES ON THE RUMP

Sampling No.	Mean Fibre Areas (μ^2) for					
	Sheep 1		Sheep 2		Sheep 3	
	P	*S*	*P*	*S*	*P*	*S*
2	865	518	450	331	504	401
4	507	352	351	255	613	340
8	550	308	285	267	421	241

The results in Table 5 show the same trends as shown by the midside samples. A comparison of relative changes in primary and secondary diameter at the midside and rump is given in Table 6, where the areas at the rump are expressed as a percentage of the area of the same fibre type at the midside.

TABLE 6

RELATIVE CROSS-SECTIONAL AREAS OF PRIMARY AND SECONDARY FIBRES AT THE RUMP AND MIDSIDE FOR THREE SAMPLING PERIODS

Sampling No.	Percentage Ratios (R/M)* for					
	Sheep 1		Sheep 2		Sheep 3	
	P	*S*	*P*	*S*	*P*	*S*
2	161	127	124	100	81	121
4	143	115	93	75	108	118
8	177	121	81	117	115	126

* Percentage ratio of mean cross-sectional area at the rump to that at the midside; *P*, for primary fibres; *S*, for secondary fibres.

In Table 6, sheep 1 shows good consistency of ratio in both primary and secondary fibres; sheep 2 is quite variable; while in sheep 3 primaries, for period 2 on the rump position, have a low value with a consequent lowering of the ratio of rump to midside areas. These fluctuations probably reflect experimental errors, especially the false correlations described by Lockart (1956). Primary and secondary fibres at both rump and midside appear to react to changes in nutrition approximately in proportion to cross-sectional area.

IV. Discussion

Both experiments indicate that efficiency does not differ appreciably between primary and secondary follicle types, and that changes in the level of nutrition need not rearrange the competitive relationships among follicles. Some alternative explanation of Lang's (1945) results therefore seems necessary. However, we must admit that variations in follicle nutrition may have been much more severe in Lang's material than in our own, and extrapolation from our results to his may not be fully justified. But the available evidence gives no indication that primary and secondary fibres differ markedly in their responses to changes in nutrition.

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BIRTHCOAT OF LAMBS AND ADULT FIBRE DIAMETER

By The Late L. W. Lockart*

(*Manuscript received November* 23, 1955)

Summary

Birthcoat hairiness is significantly correlated with adult fibre diameter variability, the coarser birthcoats being more variable. Birthcoat grade is not correlated with average fibre diameter, but is strongly correlated with the difference between diameters of primary and secondary fibres and with variability of primary, but not of secondary, fibres. A correlation of 0.83 was found between birthcoat grade and primary-secondary diameter difference in the adult.

I. Introduction

Birthcoats of Merino lambs show a wide variation in hairiness. Since this is a characteristic easily distinguished in early life it may be of use to know whether lambs with different types of birthcoat differ in the type of fleece they carry as adults.

Observations on birthcoat fibre types were begun by Duerden (1927), who recorded differences in size and shape of fibres from lambs. Dry and co-workers have developed this study in an effort to find the developmental pattern of the follicle population (e.g. Dry 1941). Fraser and his colleagues have expanded these observations and derived theories to account for the size and shape of the birthcoat fibres. The two main theories involved in the interpretation of the birthcoat types are: that follicles are in active competition for a limiting "substrate"; and that the ability of follicles to compete for this substrate varies and is related to the time of initiation of the particular follicle (Fraser 1952, 1953). The curve relating efficiency to time of initiation is thought to be genetically controlled, and variable between lambs. This variation, together with follicle competition, is supposed to generate the different birthcoat types. From the results of Fraser, we would expect a hairy birthcoat to have large, variable primary fibres and to have secondary fibres slightly smaller than average owing to the greater competitive efficiency of the large primary fibres.

According to Fraser's efficiency concept, follicles are expected to retain their relative efficiencies in the mature animal irrespective of nutritional level. This is in contrast to the conclusions of Lang (1945), who found that in some "tender" wools the thicker fibres were less affected than the

* New South Wales Department of Agriculture, Agricultural Experiment Station, Trangie, N.S.W. Mr. Lockart was killed in an aircraft accident in May 1955. This communication was compiled, from unpublished notes and documents, by F. Morley, who wishes to thank Dr. B. F. Short and Dr. A. S. Fraser for assistance.

finer ones. The break in the staples studied was assumed to be caused by nutritional stress, which may not have been the case. Data of the author (Lockart 1956) support the hypothesis of Fraser that fibres respond to a change in nutrition in proportion to their size.

Schinckel (1951) found that in the South Australian Merino a coarse birthcoat was associated with slightly fewer crimps per inch and more variable fibre diameter in the adult fleece. There was no change in mean fibre diameter.

Rendel (1954) has pointed out that the improved Welsh Mountain, the Romney, and the strong-wool Merino can all produce a similar type of birthcoat yet have quite different adult fleeces. This he attributed to the similarity at birth of the ratio of primary to secondary fibres in the lambs of each breed whereas, in the adult, ratios are far apart. In the Merino with its ratio of S/P of about 20/1, the primary fibres have little effect on the adult fleece, whereas in the Romney with a ratio of about 6/1 they are more important.

Morley (1955), using sheep from the Trangie Experiment Station flock and the same system of scoring as used in this study, found a significantly positive, but small phenotypic correlation between birthcoat and greasy fleece weight and the same for clean fleece weight, while there was a small negative correlation between birthcoat and crimps per inch. Yield, staple length, fold score, and body weight were not significantly correlated with birthcoat. Genetic correlations followed the same pattern. These estimates were made with 657 degrees of freedom.

We would expect then that lambs with a hairy birthcoat will develop into sheep having a big difference in diameter of primary and secondary fibres; that the type of birthcoat is an inexact index of S/P ratio in the adult; and that mean fibre diameter will be independent of birthcoat, but that in sheep with large primary fibres (and hairy birthcoats), secondary fibre diameter will be depressed.

II. Methods and Material

Eighty-two unculled Merino ewes born during February-March 1952 were studied. These ewes were progeny of parents selected for or against clean fleece weight and crimps per inch. They are therefore expected to be more variable in some characteristics than a random sample of ewes from the Trangie flock.

Birthcoats were scored within 1-3 days of birth, a score of 7 being given to the most hairy type, 1 to the least hairy. Skin sections were collected by trephine when sheep were approximately 16 months old. Fleece characteristics were determined on fleeces taken at the second shearing when sheep were approximately 17 months old.

Diameters of fibres were determined from skin sections, 50 primary and 50 secondary fibres being measured on each sheep. Average fibre diameter was weighted according to S/P ratio.

III. Results and Discussion

The correlation between birthcoat and mean fibre diameter was 0.02 and between birthcoat and coefficient of variation of fibre diameter 0.34, the latter value being highly significant.

Variation between fibre diameters can arise from three sources: within primary fibres, within secondary fibres, and the difference between secondary and primary fibres. Because of the much greater number of secondaries the variation within secondaries will be the most important source. Table 1 contains the mean fibre cross-sectional areas and mean standard deviations for primary and secondary fibres by birthcoat grades.

Table 1

Average fibre cross-sectional area and standard deviation (μ^2) according to birthcoat grade

Grade	No.	Cross-sectional Area of Primary Fibres		Cross-sectional Area of Secondary Fibres	
		Mean	S.D.	Mean	S D.
1	10	573	149	491	122
2	6	639	160	499	116
3	15	625	174	479	132
4	17	702	204	478	135
5	28	779	244	463	130
6	5	903	317	393	127
7	1	811	364	567	172

The increased variability with increase in hairiness is evidently due to an increase in difference between primary and secondary diameters, and to increased variation within primary fibres. There is little change in the variability of secondary fibres. Since primary fibres constitute a minor proportion of total fibres, the correlation between birthcoat and primary fibre diameter is obscured if mean diameter only is considered. However, in the birthcoat the higher proportion of primary fibres may result in a positive correlation between fibre diameter and birthcoat.

In Table 2 are given some correlations between birthcoat grade and primary and secondary fibre measurements.

The correlation between birthcoat and difference in primary and secondary fibre diameters is exceptionally high, and is probably close to the upper limit set by the accuracy of the gradings and measurements. This correlation appears to be the main sign in the adult Merino fleece of the type of birthcoat.

Before dealing with the interpretation of these results it may be as well to consider some of the errors inherent in the observations. These may be divided into three main groups. First are those due to permanent environmental effects on the follicle population. For example, if a lamb is

subjected to poor conditions in early post-natal life the follicle population may be permanently altered. Second come those temporary differences due to the momentary metabolic state of the animal which may cause, for example, primary and secondary diameters to change together.

The third type of error comprises false correlations introduced by the techniques. When a skin sample is taken with a trephine there will be some variation in the area taken. This could be caused by different amounts of stretching of the skin when the animal is lying on the sampling table,

TABLE 2

CORRELATIONS INVOLVING BIRTHCOAT GRADE AND VARIOUS MEASUREMENTS OF PRIMARY AND SECONDARY FIBRES

n_{p+s}/n_p, ratio of number of all fibres to number of primary fibres; $\overline{d}_p$, mean diameter of primary fibres; $\overline{d}_s$, mean diameter of secondary fibres; $\overline{d}_p - \overline{d}_s$, difference in primary and secondary fibre diameter; D_p, number of primary fibres per unit area of skin; D_s, number of secondary fibres per unit area of skin; *BC*, birthcoat grade

Character	n_{p+s}/n_p	$\overline{d}_p$	$\overline{d}_s$	$\overline{d}_p - \overline{d}_s$	D_p	D_s
$\overline{d}_p$	0.10	—				
$\overline{d}_s$	−0.24	0.21	—			
$\overline{d}_p - \overline{d}_s$	0.24	0.82	−0.39	—		
D_p	−0.19	−0.17	−0.26	−0.01	—	
D_s	0.55	−0.04	−0.39	0.29	0.70	—
BC	0.16	0.45	−0.11	0.83	−0.10	0.07

Min. sig. diff.: $P = 0.05$, 0.22.
$P = 0.01$, 0.28.

and perhaps by the manipulation of the trephine varying slightly from sheep to sheep. Both primary and secondary follicle density estimates would be affected so that, for example, portion of the correlation of 0.70 between the density of primary fibres and that of secondary fibres may have been generated because the errors were correlated. The measurement of fibre diameter is not free from the same type of error, for if the skin sections were not cut at right angles to the fibre axis, the apparent cross section of both primary and secondary fibres would be too large. This last type of error could be most important.

Although the secondary fibres measured include many that were not present in the birthcoat, it seems a reasonable assumption that the later-developing follicles would be slightly smaller than those in the birthcoat (Fraser 1952). Random variation in diameter of the late-developing secondaries would disturb all the correlations and the interpretation. The high correlations obtained make this seem an unlikely source of important errors.

All the sources of error mentioned above should be random with respect to birthcoat grades. The results as they stand seem to permit of

only one interpretation: that the observer scoring the birthcoats was scoring for a difference in length of the inner and outer coat of the lamb and that this difference can be caused by independent changes in the size of either primary or secondary fibres, the former being the more spectacular.

If the birthcoat score were allotted on the size of primary fibres alone, the secondary fibres would be expected to show a slight increase in diameter with increasing hairiness of the birthcoat, since the diameters of primary and secondary fibres are here positively correlated (although this correlation could be in part a reflection of the third type of error). Since the correlation of birthcoat score and secondary fibre diameter is negative (although non-significant), secondary fibre diameter must have, *per se*, an effect on the score. That this is so is shown by the correlation of -0.39 between secondary fibre diameter and the difference in primary and secondary diameters. The greater effect, however, is due to the primary fibres, which have a correlation of 0.82 with the difference in diameter of the two types. The positive correlation (0.21) between primary and secondary diameters is small enough to allow these opposing effects to occur. The partial correlation between birthcoat score and primary fibre diameter, independent of secondary diameter, is 0.49, and for secondary diameter independent of primary is -0.24. If mean fibre cross-sectional area is used instead of mean diameter, the corresponding partial correlations are 0.50 and -0.30 respectively.

The density of secondary fibres is negatively correlated with diameter of secondary fibres, presumably through the effect of competition. Similarly the density of primary fibres is negatively correlated with secondary diameter and to a less extent with primary diameter. But density of secondary fibres apparently exerts little or no effect on primary diameter. Primary follicles are apparently affected by competition far less than are secondary follicles. Such results seem consistent with the theories of Fraser (1952, 1953) and Fraser and Short (1952) relating to "efficiency" of follicles. However, the results should be accepted with caution in view of the third type of error referred to above.

Finally, these results demonstrate that birthcoat grade would be a most useful index of adult fibre variability in sheep in which primary fibres constitute a large proportion of the adult fleece. Since in the Merino the S/P ratio is high, the value of birthcoat as a selection index may be limited. Nevertheless the correlations are sufficiently high to warrant further investigation of genetic relationships.

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VARIATION IN WOOL PRODUCTION PER UNIT AREA OF SKIN

By The Late L. W. Lockart*

(*Manuscript received October* 10, 1955)

Summary

An examination of available published data does not support the claim by Galpin (1947) that production of wool per unit area of skin is a constant under optimal conditions.

I. Introduction

In a recent paper (Morley, Lockart, and Davis 1955) the greasy wool production per unit area of skin was shown to have a coefficient of variation of 18 per cent. in 66 Merino rams and 14 per cent. in 82 Merino ewes at Trangie. The production of an individual was relatively constant between periods despite differences between individuals in age and environment. Galpin (1947) stated that ". . . under good growing conditions, for the same region, all sheep produce the same weight of wool per sq. cm. per day . . .". Although the sheep at Trangie were not under optimal growing conditions the consistent differences between sheep suggested that Galpin's statement was unlikely to be generally valid. Further, Morley (1956) gave estimates of genotype-plane of nutrition interactions which were zero for fleece weights but substantial for body weights. Since skin area is a function of body weight, and one of the two planes of nutrition could be described as very nearly optimal, there were clear differences in production of wool which were independent of body weight and therefore of skin area.

If Galpin were correct one would expect fleece weight to be almost completely determined by body weight and fold score. In the data of Morley, Lockart, and Davis (1955) only about 25 to 30 per cent. of the variance of greasy fleece weight was attributable to linear relationships with these two independent variables. While non-linear relationships and suboptimal conditions may have affected the correlations, constancy of production per unit area seems unlikely.

These findings led to an examination of Galpin's data, in an attempt to reconcile the apparent contradictions.

II. Examination of Galpin's Data

In paper I (Galpin 1947, p. 276) four sheep groups in their first adult summer were used. Results were not tabulated but plotted (Ibid., Figure

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TABLE 1

SKIN AREA, WOOL WEIGHT PER DAY, AND WOOL WEIGHT PER UNIT AREA PER DAY FOR INDIVIDUAL SHEEP

Data from Galpin's (1947) Figure 1(*a*).

Weight per Day (mg)	Area (sq. cm)	Weight per Unit Area per Day (mg/cm²/day)
1941 *Group*		
13	10.0	1.3
17	12.5	1.4
12	11.5	1.0
12	8.0	1.5
11	8.5	1.3
9	8.0	1.1
7	7.0	1.0
Coeff. of variation, 16%	Mean ± s.d. = 1.2 ± 0.20	
1942 *Group*		
22	15.0	1.5
21	12.5	1.7
16	10.0	1.6
Coeff. of variation, 6%	Mean ± s.d. = 1.6 ± 0.10	
1943 *Group*		
15	9.0	1.7
12	7.0	1.7
14	9.5	1.5
13	9.5	1.4
12	8.5	1.4
12	5.5	2.2
11	7.5	1.5
11	8.0	1.4
Coeff. of variation, 17%	Mean ± s.d. = 1.6 ± 0.27	
1944 *Group*		
16	11.0	1.5
14	9.5	1.5
14	10.0	1.4
11	7.0	1.6
10	6.0	1.7
9	8.0	1.1
9	5.0	1.8
9	7.5	1.2
8	7.0	1.1
7	5.0	1.4
6	6.5	0.9
Coeff. of variation, 20%	Mean ± s.d. = 1.4 ± 0.28	
All Groups		
Coeff. of variation, 20%	Mean ± s.d. = 1.43 ± 0.28	

1(*a*)). The coordinates of these points have been read from the graph, as nearly as possible, and Table 1 constructed. Twelve sheep were supposedly derived from the 1944 drop, but only 11 points are given on the graph.

All groups show a substantial coefficient of variation which, if the conclusion is true that all sheep produce the same weight of wool per square centimetre per day, must be attributed to experimental error. This does not seem possible. The justification for this conclusion is supposed to be given by the fact that the points for three sheep groups (1941, 1942, and 1944) lie about a regression line passing through the origin. This actually is no justification of the statement that all sheep produce a constant weight of wool per square centimetre per day. It is quite possible for this regression to pass through the origin, but for the points to have

TABLE 2

ANALYSIS OF VARIANCE OF GALPIN'S (1948) TABLE 4

Source of Variance	D.F.	S.S.	M.S.	F	$F_{0.05}$
Between sheep	10	2.42	0.242	3.51	2.4
Between years	2	0.82	0.410	5.94	3.5
Remainder	20	1.38	0.069		
Total	32	4.62			

a very wide scatter. The scatter of points shows the variation in production per square centimetre, which is in fact considerable, as can be seen from Table 1. In paper II (Galpin 1948, p. 307), the same argument applies to the data of number of fibres per unit area at 7 months plotted against the number at 1 month. The relationship of N_7 to N_1 is not constant; the range of values of N_7/N_1 seems to be from about 0.4 to 0.9, a wide range. The value of 0.75 is an average value only.

Section 3 of paper II (Galpin 1948) deals with the percentage of skin area covered by fibre. Galpin's Table 4 (1948, p. 308) gives the estimated percentage areas of skin covered by fibre for 11 sheep in three successive summers. These are stated to be calculated by multiplying the mean fibre cross-sectional area by the number of fibres per unit area. From the text, however, one must conclude that the results of Galpin's Table 4 are represented by the analysis of her Appendix Table 7. The results of an orthodox analysis of variance, shown in our Table 2, do not agree with those of Galpin's Appendix Table 7.

Both year and sheep effects were significant, as might be expected from examination of the data. Therefore Galpin's conclusion is not supported by her data, and one may conclude that the percentage of skin area covered by fibre is not constant. This finding has obvious implications for Galpin's discussion on fibre length, but these will not be considered here.

III. Discussion

The concept of constancy of production per unit area has important implications in selection for efficiency of wool production. Since metabolic rate is a function of surface area, if production per unit area were constant, selection for production per unit of food intake would be virtually impossible at high levels of nutrition. Fortunately the available data suggest that there is considerable variation in production per unit area, even under good conditions.

The argument may be advanced that conditions were not optimum in any of the experiments considered, and that differences noted reflected differences in food supply, efficiency of utilization, parasitism, or some unknown factor. Such an argument might be advanced against any experiment performed, but it would soon become unrealistic. From the genetic point of view it becomes irrelevant. Selection should surely be directed towards efficiency of utilization, and resistance to parasites or other adverse factors, including malnutrition. Skin area may be a useful index of feed consumption, and production per unit area a useful index of efficiency of production. But for the present there seems to be reasonable justification for regarding this characteristic, not as a constant, but as a variable with genetic and environmental components of variance whose relative importance may or may not alter with different levels of nutrition.

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Printed by C.S.I.R.O., Melbourne